

A REVISION OF THE *AMPHISTOMATA* OF MAMMALS

BY

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(Received for publication 12 January, 1922)

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* Species in the Museum, Liverpool School of Tropical Medicine.

INTRODUCTION

The publication by Stiles and Goldberger (1910) of their monograph on the 'PARAMPHISTOMOIDEA' called forth hostile criticism from many writers, notably Braun (1911), Odhner (1911), and Looss (1912). The chief objection of these authors to Stiles and Goldberger's classification is that they ignored the recent attempts that had been made to classify the Trematodes by using affinities in the lymphatic and excretory systems as a basis. Although not agreeing with the classification of Stiles and Goldberger, none of the above writers formulated an alternative system, and although Looss in his article of 1912 says he has been several years trying to group the Amphistomes on the comparative features of the lymphatic, excretory and copulatory systems, this work has not been published yet, so far as the writer is aware. The result is that the confusion caused by Stiles and Goldberger's multiplication of genera, etc., still exists. Stunkard (1917), in a resumé of the group, makes a 'provisional' attempt at reclassification, but as he did not examine any material except three or four species from American fish, for which he makes two new genera, he is unable to discuss whether many of the existing species and genera are valid or not. All that he has done is to remove Stiles and Goldberger's family names, leaving some of their sub-family and their generic names; to add a sub-family of Looss containing one of his own genera, one of Looss', one '(Gen. nov.) *spinulosum*,' and 'Genera of uncertain position'; and to recommend a new sub-family for *Balanorchis* and another sub-family for his own genus *Zygocotyle*. Such a procedure cannot be regarded as improving matters.

It is probable that Looss' suggestion to classify the members of the group on the minute anatomy of the lymphatic, excretory, and copulatory systems is sound, but it appears to be too complicated for practical purposes.

In view of the opportunity presented by the large collection of Amphistomes in the Museum of the Liverpool School of Tropical Medicine, the writer decided to undertake a revision of the group with the object of providing a working classification. This is not based on minute histological study but on easily ascertained anatomical characters, and some of the divisions used by Stiles and Goldberger (e.g., the three families *Gastrodiscidae*, *Paramphistomidae*, and *Gastrothylacidae*) have been retained because they serve to divide the group on easily distinguished external

characters, and are hence of practical use. It is realised that the present attempt at classification does not take cognizance of the standards required by the more advanced systematists such as Looss and Odhner, but it is claimed for this system that it is reasonably simple and consistent, and, so far as the Amphistomes of mammals are concerned, enables a species to be determined with considerable accuracy.

Looss also draws attention to the fact that Stiles and Goldberger failed to make any allowance for variation due to difference in age or the state of contraction of specimens, and have made many species on unsound data in consequence. Throughout the present work these factors have been investigated as fully as possible, and an attempt has been made to show to what extent they influence the appearance of the several species of the group. In their monographs Fiscoeder and Stiles and Goldberger both deal so fully with the synonymy, that it has not been considered worth while to go back beyond these authors.

NOTE.—The reader is referred to Cohn (1904), Daday (1907), Looss (1912), and Stunkard (1917), for the most recent information regarding Amphistomes parasitic in hosts other than mammals.

AMPHISTOMATA, Rudolphi, 1801, e.p., Nitsch, 1819

Definition.—*Digenea*: two suckers, the anterior surrounding the mouth and the posterior terminal or ventro-terminal behind the genitalia; gut forked; excretory pore opening dorsally towards the hinder end; testes generally in front of ovary; almost always thick worms more or less circular in section.

KEY TO FAMILIES

- | | | | | | | | | |
|----|---|-----|-----|-----|-----|-----|-----|-------------------------|
| 1. | Body usually flattened and divided into anterior and posterior portions; ventral pouch absent | ... | ... | ... | ... | ... | ... | <i>Gastrodiscidae</i> |
| | Body usually conical and not divided into anterior and posterior portions | | | | | | 2 | |
| 2. | Ventral pouch absent | ... | ... | ... | ... | ... | | <i>Paramphistomidae</i> |
| | Ventral pouch present | ... | ... | ... | ... | ... | | <i>Gastrothylacidae</i> |

Family PARAMPHISTOMIDAE, Fiscoeder, 1901.

Definition.—*Amphistomata*: body not divided into two portions; ventral pouch absent.

KEY TO SUB-FAMILIES

1.	Oral diverticula absent	...	...	...	...	...	<i>Paramphistominae</i>
	Oral diverticula present	...	...	...	...	...	2
2.	Oral diverticula double	...	...	...	...	...	<i>Cladorchinae</i> *
	Oral diverticula single	..	...	...	...	...	<i>Stephanopharynginae</i>

Sub-family *PARAMPHISTOMINAE* (Fischöeder, 1901), s.str., Stiles and Goldberger, 1910.

Definition.—*Paramphistomidae*, without oral diverticula.

KEY TO GENERA

Genital sucker absent	...	...	...	...	...	<i>Paramphistomum</i>
Genital sucker present	...	...	...	...	...	<i>Cotylophoron</i>

Genus *Paramphistomum* (Fischöeder, 1901), s.str., Stiles and Goldberger, 1910.

Definition.—*Paramphistominae*, without a genital sucker.

Type species *Paramphistomum cervi* (Zeder, 1790), Fischöeder, 1901.

KEY TO SPECIES

A.	Testes in tandem†	...	...	...	...	...	...	1
B.	Testes diagonal†	...	...	...	...	...	...	6
1.	Testes lobed	...	...	...	...	...	...	2
	Testes not lobed	...	...	...	...	...	...	5
2.	Testes with two lobes	...	...	...	...	...	<i>P. gigantocotyle</i>	
	Testes with more than two lobes	...	...	...	...	...	...	3
3.	Anterior sucker deeply retracted	...	...	...	...	...	<i>P. pisum</i>	
	Anterior sucker not retracted	...	...	...	...	...	...	4
4.	Laurer's canal opens posterior to excretory pore	...	...	...	...	...	<i>P. cervi</i>	
	Laurer's canal opens anterior to excretory pore	...	...	...	...	...	<i>P. orthocoelium</i>	
5.	Laurer's canal opens posterior to excretory pore	...	...	...	...	...	<i>P. liorchis</i>	
	Laurer's canal opens anterior to excretory pore	...	...	...	...	...	<i>P. wagandi</i>	
6.	Testes lobed, Laurer's canal posterior to excretory pore	...	...	...	...	...	<i>P. explanatum</i>	
	Testes not lobed, Laurer's canal anterior to excretory pore	...	...	...	...	...	<i>P. buxifrons</i>	

* Cohn (1904) created a new sub-family *Diplodiscinae*, all the members of which are found in Amphibians and Reptiles. This sub-family has two oral diverticula and has no constant characters by which it may be distinguished from *Cladorchinae*.

† Refers to mature worms, because in young specimens of *P. cervi*, the testes are sometimes found to be slightly diagonally arranged; by this it is meant that the testes are only slightly out of the mid-line, so that the antero-posterior axis of the worm always intersects both testes, but one testis always lies so far in front of the other that a transverse line can be drawn between them without touching either. In young specimens of *P. explanatum*, the testes lie one on each side of the mid-line, so that the antero-posterior axis passes between them without touching either, but one testis is only slightly in front of the other, so that a transverse line intersects both testes. In mature *P. cervi* the slightly diagonal arrangement is not seen, and the testes appear in tandem, whereas in mature *P. explanatum* the testes are definitely diagonal.

Paramphistomum cervi (Zeder, 1790), Fiscoeder, 1901.

SYNONYMY :—

- Paramphistomum gracile*, Fiscoeder, 1901.
Paramphistomum bothriophoron (Braun, 1892), Fiscoeder, 1901.
Paramphistomum microbotrium, Fiscoeder, 1901.
Paramphistomum bathycotyle, Fiscoeder, 1901.
Paramphistomum epiclitum, Fiscoeder, 1904.
Paramphistomum papillosum, Stiles and Goldberger, 1910.
Paramphistomum papilligerum, Stiles and Goldberger, 1910.
Paramphistomum indicum, Stiles and Goldberger, 1910.

The following is a list of the material available :—

1. Ten bottles from the stomach of bullocks killed in the military slaughter-house at Sierra Leone, West Africa.
2. Two bottles from the stomach of bullocks killed at Khartoum, Sudan.
3. One bottle from the stomach of a bullock killed at Yola, Northern Nigeria.
4. One bottle from the stomach of a bullock killed at Zomba, Nyasaland.
5. One bottle from the stomach of a bullock killed at Blantyre, Nyasaland.
6. One bottle from the stomach of a bullock killed at Accra, Gold Coast.
7. One bottle from the stomach of a bullock killed at Nairobi, Kenya Colony.
8. One bottle from the stomach of an antelope (*Cobus* sp.) shot in the Northern Territory of the Gold Coast.
9. One bottle from the stomach of a Roan shot in Nyasaland.
10. One bottle from the stomach of a bullock in England.
11. Two bottles, host and locality ?

Many of the above collections comprised some hundreds of specimens, and other worms of the same group occurred along with them in several instances.

EXTERNAL ANATOMY

Size and shape. The size and shape exhibit such infinite variation as to be of little diagnostic value (Plate V).

Cuticular papillae. Fiscoeder (1903) states that in some cases he found a number of small papillae of varying size on the cuticle surrounding the oral opening of *P. cervi*, and he does not agree with von Blumberg (1871) that these papillae are always present. The present investigation is in accordance with Fiscoeder's view, as they were found in some specimens and not in others.

Other points usually discussed under External Anatomy will be included under Internal Anatomy, because their full consideration involves details that can only be made out in sections or in cleared specimens.

INTERNAL ANATOMY

Muscular system. The points requiring special mention in this system will be referred to under special organs.

Nervous system. This system was not investigated as it has not been used in specific diagnosis.

Excretory system. Fiscoeder (1903) describes and figures the excretory bladder of *P. cervi* as being of a definite shape, with thin smooth walls and with the excretory pore opening well in front of the bladder. Examination of a large number of sectioned specimens leads one to the conclusion that a definite form cannot be assigned to the excretory bladder, which varies according to its degree of distension. The position of the excretory pore in relation to the bladder is also found to vary with the age of the individual; in those with no eggs in the uterus, the pore opens dorsally or dorso-posteriorly of the bladder, and as the uterus gradually fills with eggs the pore appears to pass further and further forward until it is seen to open well in front of the bladder. This point is fully discussed under *P. explanatum*, and as *P. cervi* is found to vary in exactly the same manner no further reference to it will be made here.

Anterior sucker. The anterior sucker may be longer than broad, circular, or even broader than long. When contracted the central canal of the sucker may be narrow; on the other hand if its external aperture is widely open, the canal may be funnel-shaped, becoming narrower towards its junction with the oesophagus. The internal surface of the oral cavity may, or may not, be furnished with small papillae, but these vary in exactly the same way as in the case of the cuticular papillae; in fact, owing to their irregular distribution, papillae may be present in some sections and absent in others of the same worm. Fiscoeder (1903) states that he found papillae in all the sectioned specimens he examined.

Oesophagus. No special mention of the muscle wall of the oesophagus of *P. cervi* is made by Fiscoeder (1903), but in describing other species, e.g., *P. dicranocoelium* and *P. cotylophorum*, he says that the oesophagus of these two worms is characteristic, because the muscle wall is thicker near the gut fork than near its anterior end; therefore the inference is that the oesophagus of *P. cervi* does not exhibit this thickening. Careful examination of five specimens of *P. cervi* cut in sagittal section gave the following results.

TABLE I.

Thickness of the muscle wall of the oesophagus of *P. cervi*.

							Near its anterior end	Near the gut fork
Specimen 1	...	...	...	...	...	...	32 μ	60 μ
Specimen 2	...	...	...	...	...	...	32 μ	40 μ
Specimen 3	...	...	...	...	...	...	20 μ	40 μ
Specimen 4	...	...	...	...	...	...	16 μ	36 μ
Specimen 5	...	...	...	...	...	..	16 μ	32 μ

In specimens 1 and 2, the oesophagus was shorter than in the other three. From the above it is clear that there is a gradual thickening of the muscle wall of the oesophagus in *P. cervi*, but it is not so marked as in the case of the other two species quoted above, and therefore it is not visible in whole specimens in *P. cervi*. Indeed, even in sectioned specimens it is difficult to appreciate with a low power, because the thickening is very gradual and not very marked, and it is only when the point is specially looked for with a high power that one realises its existence. In the collection of material from the *Cobus* sp. of antelope in the above list, some specimens were found which showed the oesophagus to be slightly bulbous even in whole worms, and on sectioning one of these the muscle wall of the oesophagus was found to be 20 μ thick at the anterior and 72 μ thick at its posterior end. Although the difference in this case is considerably greater than among the above specimens, the writer does not consider it sufficiently marked to be taken as a specific difference, and merely records it as a probable variant of *P. cervi*.

The intestine. Both the degree of convolution and the precise point of termination of the gut caeca are regarded by Fiscoeder (1903) as important points in differentiating between species closely allied to *P. cervi*. These two points were examined in about 150 specimens cleared in carbolic and in about 40 sectioned specimens. Fifty specimens were taken from one bottle, which were chosen on account of their close similarity in external appearance, as it was thought by this means that variation due to artificial influences could be almost entirely eliminated. The result of the examination of these fifty specimens showed that the caeca were nearly straight in some cases and in others were distinctly convoluted, and

between these two extremes there were others with all degrees of convolution of the gut, which indicates that a variable species is being dealt with. This view was further supported by noting a different amount of convolution of the two caeca in the same worm in several instances. The point of termination of the two caeca also varied considerably; in some they ended quite clear of the anterior border of the posterior sucker, and in others they extended as far as the middle of the posterior sucker. In collection No. 10 of the above list, the worms were more fully extended than in any other collection, and in one of these specimens the gut was found to end 1.6 mm. in front of the anterior border of the posterior sucker. All gradations between the two extremes were seen, and in a few worms the caeca ended at different levels on the two sides. The remaining specimens which were not so uniform in size and shape were found to vary in the same way. It is also stated that the gut caeca terminate in a dorsally directed blind end. This was found to be so in most cases, but three specimens were seen in which the terminal part of the caeca ran ventrally. It is considered, as a result of these findings, that small variations in the gut caeca are not reliable points on which to separate species.

Posterior sucker. The ratio of the diameter of the posterior sucker to the length of the worm is used in many instances as a distinguishing feature. For the purpose of examining this character eighty-nine worms from one bottle were measured; all of the specimens used were fixed in a well-extended condition, differences in length from artificial causes such as shrinking being thus practically eliminated. In these eighty-nine specimens the ratio of the diameter of the posterior sucker to the length of worm varied greatly, all intermediate figures between 1:8 and 1:3.5 being found, and the variations were so gradual that it was found impossible to draw a dividing line at any point in the series. A large number of worms from other bottles were also measured in the same way, and as these were in different degrees of contraction the variation was found to be even greater than in the above series; in one strongly contracted example the ratio of sucker to length of worm was only 1:2.5. The collection obtained from England (No. 10) consisted of twelve specimens, which were part of the collection mentioned by Pillers (1922). They were all fully extended and presented a very uniform appearance externally, both in size and shape. Five of these specimens were cleared in carbolic and it was found that the diameter of the posterior sucker in proportion

to the length of the worm in the five specimens was as follows: 1:9.5, 1:7, 1:5.7, 1:5.4, 1:4.75. All of these specimens were gravid, and as they only varied from about 11 mm. to 10 mm. in length, it is obvious that the size of the sucker varies quite apart from the age and size of the worms. According to Pillers these worms are very uncommon in England, so it is improbable that more than one species is present in this small collection. All of these worms were cleared in carbolic acid, so that the general anatomical details were sufficiently clear to render it certain that only one species was being dealt with, and it was noted that the other characters used as distinguishing features between species of this group did not always occur in worms with a corresponding size of sucker. For instance, a worm with a sucker only one-eighth the length of the worm, and hence belonging to *P. gracile* on this account, might have its other diagnostic points more closely allied to *P. cervi* or any other of the species to be discussed below. This mixture of characters of more than one type could be indefinitely extended until the species became inextricably confused. It is considered, on account of the above observations, that the ratio of the posterior sucker to the length of the worm is much too variable to be used as a diagnostic character.

Genitalia. Testes. The size and shape of these organs and their relations to one another and to other structures were found to vary somewhat, depending on differences in age and on the degree of contraction in which the worms happened to be when fixed. One testis always lies behind the other, in or near the mid-line; as a rule one testis is directly behind the other, but in young specimens with small testes they are sometimes slightly diagonally placed. When the testes have grown, however, this diagonal arrangement is no longer so obvious. Also in young worms, and even in fully extended examples with eggs in the uterus, there is sometimes a distinct interval between the two testes up to as much as 1 mm. In these instances the testes are circular in outline. On taking a series of worms of gradually increasing age and degree of contraction, the testes are found to come closer and closer together until they touch; after this they tend to become flattened with consequent extension laterally and dorso-ventrally, so that they appear oblong in shape and their borders approach nearer the periphery; in extreme cases they even cause a bulging of the external surface of the worm. The relation of the posterior testis to the posterior sucker also varies considerably; in young worms and well-extended adults the hinder testis lies altogether in front of the posterior

sucker, but in worms not so well-extended the posterior border of the hinder testis reaches, or overlaps, the anterior border of the sucker. The testes are always divided into lobes, which are more distinct in young worms than in older ones. These conclusions are based on the examination of over forty specimens.

Another point of some interest was that three or four specimens were found with the uterus quite full of eggs and the testes small and indefinite. From this it seems possible that the testes atrophy after fulfilling their functions.

Vas deferens. Fiscoeder (1903) made an arbitrary division of this organ into three principal parts dependent on the anatomical characters of each part, and as this division is very useful for purposes of description his nomenclature will be followed in the present paper.

The three portions of the vas deferens are as follows :—

1. *Vesicula seminalis.* = A thin-walled coiled tube formed by the junction of the two vasa efferentia.
2. *Pars musculosa.* = The continuation of the vesicula seminalis, furnished with a fairly thick muscular wall.
3. *Pars prostatica.* = A shorter portion of the tube surrounded by a collection of large cells, the prostatic cells.

The pars prostatica leads into a duct known as the Ductus Ejaculatorius, which unites with the termination of the uterus within the genital papilla, and which is known as the Ductus Hermaphroditicus.

The vesicula seminalis varies greatly in size and amount of convolution in different specimens. These variations depend on several factors, such as the degree of contraction of the worm, and whether the vesicula is empty, partly filled, or fully packed with spermatozoa when the worm is killed. The pars musculosa is liable to vary from the same causes, and to these must be added variation due to the state of contraction of its own muscular wall. The muscle wall of the pars musculosa is composed of two layers, an outer longitudinal layer, and an inner circular layer, so that contraction or relaxation of one or both of these layers can cause considerable variation in the length, diameter, amount of convolution of the duct, or the proportionate thickness of the two muscle layers. Both the vesicula seminalis and the pars musculosa coil freely on themselves and on each other, so that their relations with each other vary greatly in different specimens, and even in different sections of the same specimen. From examination of a large number of sectioned specimens,

the writer has come to the conclusion that the relations of the vesicula seminalis and the pars muscosa are so variable that it is not possible to assign any special type of relation between these two parts to any one species as Fiscoeder does in several instances. The pars prostatica varies considerably in size and shape; this fact is clearly brought out in Table II, which is compiled from the measurement of fifteen individuals cut in sagittal section and mounted serially; the maximum measurements are given in every case.

TABLE II.

The length and breadth in microns of the pars prostatica of fifteen specimens of *P. cervi*.

	Length	Breadth		Length	Breadth
1	178	178	9	436	257
2	218	138	10	475	297
3	218	218	11	535	396
4	257	198	12	594	317
5	277	198	13	594	396
6	297	178	14	594	475
7	317	138	15	594	495
8	317	218			

This table shows a regular gradation of sizes from the smallest to the largest, and from this it is concluded that it is not possible to separate species on this character.

Genital pore. The genital pore usually lies about opposite the gut fork or a little behind it, the variation in position depending on the length and course of the oesophagus, which naturally has a direct effect on the position of the gut fork. But in one sectioned specimen which was fully grown and very much contracted, and in consequence only about 4 mm. in length, the genital pore was only $\frac{1}{4.8}$ of the body length from the anterior end of the worm, and it lay opposite the junction of the middle and posterior thirds of the anterior sucker, that is, far in front of the gut fork. This is not in agreement with the statement of Fiscoeder (1903) who, in his description of *P. cervi*, says:

‘Die Geschlechtsöffnung liegt am hinten Ende des vordern Körperdrittels in der Höhe oder kurz hinter aber niemals vor der Gabelstelle der Darmschenkel.’

Genital atrium and genital papilla. These two structures are used extensively in specific diagnosis both by Fiscoeder (1903) and by Stiles and Goldberger (1910). The papilla is composed almost wholly of muscle, and the atrium is surrounded by a special thickening of the subcuticular layer. Accordingly, both are liable to great alterations in form, and further, the papilla is capable of being withdrawn deeply into the body of the worm with resultant deepening of the genital atrium, or else it can be completely extruded through the genital pore, in which case the genital atrium disappears. As would be expected, many worms show intermediate stages between these two extremes. The variations of the genital apparatus are fully discussed in *P. explanatum* (see fig. 2), and as exactly the same type of variations are found in *P. cervi* the reader is referred to *P. explanatum*. The conclusions to be drawn from these facts are that the presence of one or two chambers in the genital atrium, or even the total absence of this cavity, or the size and shape of the genital papilla, are purely a matter of chance and are of no use in distinguishing various species. If Fiscoeder's figures (1903) of *P. cervi* are referred to, it will be noted that in fig. 1 the pore is shown as a small cavity with no sign of the papilla protruding, whereas figs. 2 and 3 show the papilla protruded through the pore and there is no sign of an atrium at all. This suggests that Fiscoeder recognised the possibility of variation in these structures without referring to it in the text. Small papillae are also described as being found on the internal surface of the genital atrium in some species and not in others. Examination of a number of sectioned specimens has shown that these papillae may be present or absent when the atrium is present, and a further fact which makes these structures still more liable to variation is that often the atrium itself is not present.

Ovary. It is recognised by all observers that the ovary may vary considerably in position in the same species. The present investigation fully bears this out.

Shell gland. This gland always lies close to the ovary, and so varies in company with it.

Vitellaria. The vitellaria appear to be the most variable of all the organs in *P. cervi*, and the number of gland groups, their size, and their distribution, undoubtedly increase considerably as age advances. But even when comparing them in over one hundred specimens in which the uterus was well filled with eggs they were found to show marked variation. Among these hundred odd specimens the anterior limits of the vitelline

glands were found to lie as far forward as the hinder end of the anterior sucker in some cases, whereas in others they did not reach as far as the genital pore, and between these two extremes all degrees were found. Sometimes in the same worm the glands did not reach the same level on both sides. The posterior limits of the vitellaria were also found to vary considerably, but as a general rule they ended a little behind the termination of the gut caeca; but this was not invariably the case, for in a few instances the vitelline follicle groups were found extending to the extreme posterior end of the worm and could be made out in the parenchyma surrounding the opening of the posterior sucker. The degree of extension of the vitellaria inwards on the dorsal and ventral surfaces also varied markedly. In some cases the glands were strictly limited to the area outside the intestines on each side, and from this limited distribution all stages of inward extension were found up to a point where the glands of the two sides were practically continuous with one another all along both surfaces. It was noted, however, that when the glands were widely spread they seemed to be sparsely distributed, and when fairly circumscribed in their distribution the groups of follicles were much more closely gathered together. Fiscoeder (1903) uses slight differences in distribution of the vitelline glands for specific diagnosis; the writer does not consider this possible, because in his series of over one hundred gravid specimens of *P. cervi* a much greater range of variation was found than Fiscoeder describes in his different species, and between the extreme limits of these variations all possible degrees were found which made it impossible to separate one species from another.

Uterus. The dorsal antero-posteriorly directed portion of the uterus is described as being more convoluted in some species than in others. After a large number of specimens were examined it was realised that the amount of convolution the uterus shows is subject to a wide range of variation in *P. cervi*. This variation was found to be dependent on two factors, first, the amount of contraction of the worm, and second, the number of eggs in the uterus. It was found that in specimens with no eggs the uterus was nearly straight, but as it became more and more filled with eggs the degree of convolution of the uterus increased also. It is therefore considered that slight differences in the amount of convolution of the uterus cannot be taken into consideration in specific diagnosis.

Eggs. Eggs taken from the uterus of several preserved specimens of *P. cervi* were found to vary considerably in size, being from 114μ in length

TABLE III.

Relations of the ovary, shell gland, Laurer's canal and excretory pore in five specimens of *P. cervi* cut in transverse section.

Specimen	A	B	C	D	E
Relations of ovary ...	To right of mid-line. In same dorso-ventral plane as shell gland. Midway between dorsal and ventral surfaces.	To left of mid-line, well towards ventral surface.	In mid-line ventro-posterior to shell gland. Slightly ventral of mid-transverse plane.	Well to right of mid-line in mid-transverse plane.	To left of mid-line: just ventral of mid-transverse plane. Just anterior to hinder border of testis.
Relations of shell gland...	In mid-line. Midway between dorsal and ventral surfaces.	Directly dorsal of ovary.	Just to right of mid-line and slightly dorsal of mid-transverse plane.	Just to right of mid-line antero-internal to ovary and just dorsal of mid-transverse plane.	Immediately dorsal of ovary.
Course of Laurer's canal ...	First dorsally to right of excretory bladder, then turns mesially and crosses to left side anterior to excretory bladder and posterior to excretory duct.	Dorsally and anteriorly on left side of excretory bladder	Dorsally and posteriorly on right side of excretory bladder.	Dorsally and anteriorly on right side of excretory bladder.	Dorsally and posteriorly on left side of excretory bladder
Opening of Laurer's canal ...	100 μ posterior to and 300 μ to left of excretory pore. 50 μ anterior to anterior border of shell gland. 250 μ anterior to base of ventral sucker.	75 μ posterior and 400 μ to the left of excretory pore. 500 μ anterior to anterior border of shell gland. 325 μ anterior to posterior border of hinder testis. 650 μ anterior to base of ventral sucker.	500 μ posterior and 625 μ to right of excretory pore. 75 μ posterior to posterior border of shell gland. On a level with base of ventral sucker.	200 μ posterior and 300 μ to right of excretory pore. Directly above shell gland. 175 μ anterior to base of ventral sucker.	500 μ posterior and 650 μ to the left of excretory pore. 100 μ posterior to posterior border of shell gland. On a level with base of ventral sucker.
Opening of Excretory pore ...	In mid-line 250 μ anterior to anterior limit of excretory bladder, and 100 μ posterior to posterior border of hinder testis.	In mid-line, 275 μ anterior to anterior limit of excretory bladder. 400 μ anterior to posterior border of hinder testis.	Slightly to left of mid-line, and vertically above left side of excretory bladder. 75 μ posterior to anterior limit of excretory bladder. On a level with posterior border of testis.	In mid-line 100 μ posterior to anterior limit of excretory bladder. 75 μ posterior to posterior border of hinder testis.	Slightly to right of mid-line and vertically above right side of excretory bladder. 125 μ posterior to anterior limit of excretory bladder. 375 μ anterior to posterior border of hinder testis.

by 60μ in breadth up to 176μ in length by 90μ in breadth. The above figures represent the extremes of size found after several specimens had been dissected; the maximum variation in eggs from a single worm was only about 10μ in length and 7μ in breadth. It is considered on this account that small differences in size of the eggs are not reliable characters for specific diagnosis, at all events when the eggs are taken from the uterus of preserved specimens. It is possible they may be more uniform in size after being laid.

Laurer's canal. The relations between Laurer's canal, the excretory bladder, and excretory pore are used by Fiscoeder (1903) in distinguishing certain species from one another. He evidently attaches great importance to these relations, because he divides the genus *Paramphistomum* into three groups on these characters, and Stiles and Goldberger (1910) have followed Fiscoeder in this respect. Fiscoeder's three groups of the genus are as follows:—

1. Laurer's canal crosses the excretory bladder completely. This means that Laurer's canal opens behind the excretory pore and in the mid-line of the worm.

2. Laurer's canal and the excretory bladder do not cross. This means that Laurer's canal opens in front of the excretory pore.

3. Laurer's canal crosses the excretory bladder incompletely. This means that Laurer's canal opens behind the excretory pore, but to the side of the mid-line, i.e., the same side as that on which the shell gland lies.

On account of the importance attached to these characters, five specimens of *P. cervi* all from one bottle and as nearly as possible similar in external appearance, were cut in transverse sections, 25μ thick, and mounted serially, so as to test the value of the above statements. The result of this investigation is shown in Table III.

Table III and Fig. 1, which consists of camera lucida drawings of Specimens A, B, and C in Table III, show that the relations of Laurer's canal to the excretory bladder and excretory pore vary considerably, and in some cases the relations of these structures do not come under any of Fiscoeder's three headings. It is probable that if more worms were examined still other arrangements would be found, but it was considered that the above five specimens sufficiently proved that these relations were unreliable for diagnostic purposes. Although only the above five specimens are included in the table, about thirty others were examined; these were cut in sagittal and coronal sections and the above results were thereby

Summarising the chief characters described by Fiscoeder (1903 and

	(1) <i>P. cervi</i>	(2) <i>P. gracile</i>	(3) <i>P. microbotrium</i>
Length	5-12 mm.	11-15 mm.	8-11 mm.
Shape	Posterior end rounded	Almost cylindrical.	Somewhat more flattened dorsally than <i>P. cervi</i> . Only slightly curved ventrally like <i>P. gracile</i> .
Relation of sucker to length of worm	1 : 4 to 1 : 5	1 : 8	1 : 4 to 1 : 5.
Genital pore	Opposite or behind gut fork, $\frac{1}{3}$ of body length from anterior end.	Well behind gut fork, $\frac{1}{4}$ of body length from anterior end.	Behind gut fork, $\frac{1}{4}$ of body length from anterior end. Has a genital atrium and more definite muscular sphincter.
Vesicula seminalis	Very broad, thin walled, in front of anterior testis.	Round canal in median plane.	Lies dorsal of pars musculosa, unlike <i>P. cervi</i> and <i>P. gracile</i> where it is behind.
Pars musculosa	0.8 to 1.0 mm. long, walls 18μ to 22μ thick, varying with its degree of fullness. Straight or slightly coiled.	500 μ to 600 μ long, walls 18μ to 22μ thick. Moderately straight.	Walls 45μ -50 μ thick: almost exclusively consisting of circular muscle with a single outer layer of longitudinal muscle. Strongly coiled.
Pars prostatica	300 μ to 600 μ in transverse diameter.	500 μ to 600 μ long by 250 μ to 350 μ broad.	500 μ to 600 μ long.
Papillae on anterior end and in 'pharynx'	On external surface and in anterior portion of 'pharynx.'	On external surface and not in 'pharynx.'	Not mentioned.
Termination of gut caeca	Dorsal to sucker.	Anterior to sucker.	Anterior to sucker.
Testes	ANTERIOR: 2 mm. to 2.8 mm. dorso-ventral. 1.5 mm. to 2 mm. transverse. POSTERIOR: 2.8 mm. to 3.5 mm. dorso-ventral. 1 mm. to 1.5 mm. transverse. Slightly on opposite sides of middle line, close to ventral surface.	ANTERIOR: Oval, 1.2 mm. by 0.7 mm. slightly dorsal. POSTERIOR: More rounded, 0.9 mm. by 1.0 mm., slightly ventral. Only lie slightly on opposite sides of median line.	ANTERIOR: 2.3 mm. to 2.5 mm. dorso-ventral. 1.5 mm. to 1.7 mm. transverse and longitudinal. POSTERIOR: As a rule somewhat larger. A little more markedly on opposite sides of mid-line. Close to ventral surface.
Vitellaria	Extend from 'Pharynx' to posterior border of ventral sucker. Extend on dorsal and ventral surfaces. In coarse groups of follicles close together.	Extend from hinder border of 'Pharynx' to anterior border of sucker; do not extend markedly on dorsal and ventral surfaces. In five groups of follicles somewhat irregularly placed.	On one side reach from posterior border of 'Pharynx' to anterior border of sucker. On other side from gut fork to middle of sucker. Similar to <i>P. cervi</i> in size and extent on dorsal and ventral surfaces.
Ovary	Close behind base of sucker, either to right or left of mid-line.	Behind posterior testis either to left or right of mid-line and slightly towards ventral surface (i.e., anterior to sucker).	Further from mid-line than in <i>P. cervi</i> and <i>P. gracile</i> .
Uterus	Portion dorsal of testes markedly wavy.	Portion dorsal of testes wavy.	As in <i>P. cervi</i> .
Eggs	145-156 $\mu \times$ 75-82 μ .	115-125 $\mu \times$ 72-80 μ .	145-150 $\mu \times$ 75-80 μ .
Laurer's canal	Runs dorsally towards anterior and opens in mid-line about level of posterior border of the hinder testis. 1-1.2 mm. behind excretory pore.	Curves posteriorly and opens at level of anterior border of ovary 1.5 mm. behind excretory pore.	Opens to one side and not in mid-line opposite anterior border of ovary 250-300 μ behind excretory pore.
Excretory bladder	Flask-shaped, close to dorsal surface. Pore opens anteriorly in mid-line. Crossed by Laurer's canal at junction of anterior and middle third.	Further from dorsal surface. Pore on a level with hinder border of posterior testis. Is crossed by Laurer's canal about its centre.	Similar to <i>P. cervi</i> . Pore in mid-line. Laurer's canal does not cross bladder.

* At the first glance *P. botriophoron* appears to have several rather marked points of difference from the other five species, e.g. pars musculosa is closely coiled; the pars prostatica is very long; and the genital atrium is large and deep, with no genital papillae.

1904), as typical of the following six species of *Paramphistomum*.

(4) <i>P. epiclitum</i>	(5) <i>P. bathycotyle</i>	(6) <i>P. botbriophoron</i> *
5-9 mm.	11-15 mm.	6-9 mm.
Anterior $\frac{1}{4}$ strongly curved ventrally, the remainder straight, as in <i>P. cervi</i> : the greatest circumference at 2nd and 3rd thirds.	Ventrally curved. Greatest transverse diameter near posterior end.	Of 4 specimens: 2 strongly curved; 2 slightly curved ventrally.
1: 3 to 1: 4.5.	In text $\frac{2}{3}$ of body length; in drawing $\frac{1}{3}$ of body length.	Not mentioned.
At junction of 1st and middle thirds. Well behind gut fork.	About middle of anterior third behind gut fork. Very little muscle surrounds it.	In middle of anterior half. Not so well developed as in other species. Like <i>P. microbotbrium</i> .
Dorsal and posterior of pars musculosa.	Lies loosely coiled between intestines.	Behind and not dorsal to pars musculosa. Closely coiled.
Walls 18μ to 22μ thick.	Ventral and anterior to vesicula, $0.6-0.75$ mm. long and $18\mu-22\mu$ thick, not coiled.	Strongly developed, not loosely coiled like others, but closely coiled. Muscle different from all other species because, unlike those which have nearly all circular muscle surrounding a single layer of longitudinal, the longitudinal is nearly as thick as the circular.
Unlike <i>P. cervi</i> , which is round, it is long $600\mu-800\mu$, and $250\mu-300\mu$ thick.	Almost globular, $400\mu-500\mu$ in diameter.	$1.0-1.2$ mm. long.
Not mentioned.	On both external surface and in 'pharynx.'	Not seen.
Beside base of sucker.	Close in front of anterior border of sucker.	Close in front of sucker.
ANTERIOR: $1.8-2.2$ mm. dorso-ventral. $0.9-1.2$ mm. longitudinal. $1.2-1.6$ mm. transverse. POSTERIOR: $2.1-2.5$ mm. dorso-ventral. $0.7-0.1$ (? 1.0) mm. longitudinal $1.6-2.0$ mm. transverse.	Longitudinal: $1.0-1.3$ mm. } Both about Dorso-ventral: $1.5-1.8$ mm. } same. Like <i>P. cervi</i> , slightly out of mid-line.	ANTERIOR: $0.7-0.8$ mm. long. POSTERIOR: $0.8-1.0$ mm. long. Both $2.0-2.3$ mm. dorso-ventral. More deeply lobed. Lie in similar position to <i>P. microbotbrium</i> .
Of different sizes and very irregular, but close together. Stretch from beginning of oesophagus as far as base of sucker. Reach further on dorsal and ventral surfaces than in <i>P. cervi</i> .	Almost from 'pharynx' to opposite anterior border of sucker. Almost confined to lateral fields only slightly encroaching on dorsal and ventral surfaces. Single follicles small.	From gut fork almost to middle of sucker and also extend on dorsal and ventral surfaces.
Between posterior testis and base of sucker and on same side of mid-line as anterior testis.	Similar position to <i>P. cervi</i> , but only slightly away from mid-line.	Between hinder testis and sucker very near ventral surface and very much to the side.
As in <i>P. cervi</i> .	Broad and filled with eggs.	Filled with eggs.
$145-155\mu \times 75-80\mu$.	$115-125\mu \times 70-75\mu$.	$125-135\mu \times 65-70\mu$.
Opens in mid-line about the level of its origin.	Runs directly dorsal and opens on a level with ovary.	Opens opposite side to ovary as in <i>P. microbotbrium</i> , opposite anterior border of shell gland.
Opens on level of middle of posterior testis $500-600\mu$ anterior to Laurer's canal. Laurer's canal crosses between 1st and 2nd thirds of bladder.	Different from <i>P. cervi</i> because it has a long anteriorly directed canal which opens opposite posterior border of anterior testis about middle of length of worm.	More rounded; in front of sucker near dorsal surface.

the longitudinal muscle of the pars musculosa is said to be very thick, and it is figured as being arranged in distinct columns; the It is conceivable that all of these conditions could be caused by one factor, viz., contraction of the longitudinal muscle of the pars

confirmed. But one point was found to be of value in regard to the relations of the opening of Laurer's canal and the excretory pore, and that is, that in species in which Laurer's canal is described as opening behind the excretory pore this is invariably the case, although the actual distance at which one pore lies behind the other varies a good deal.

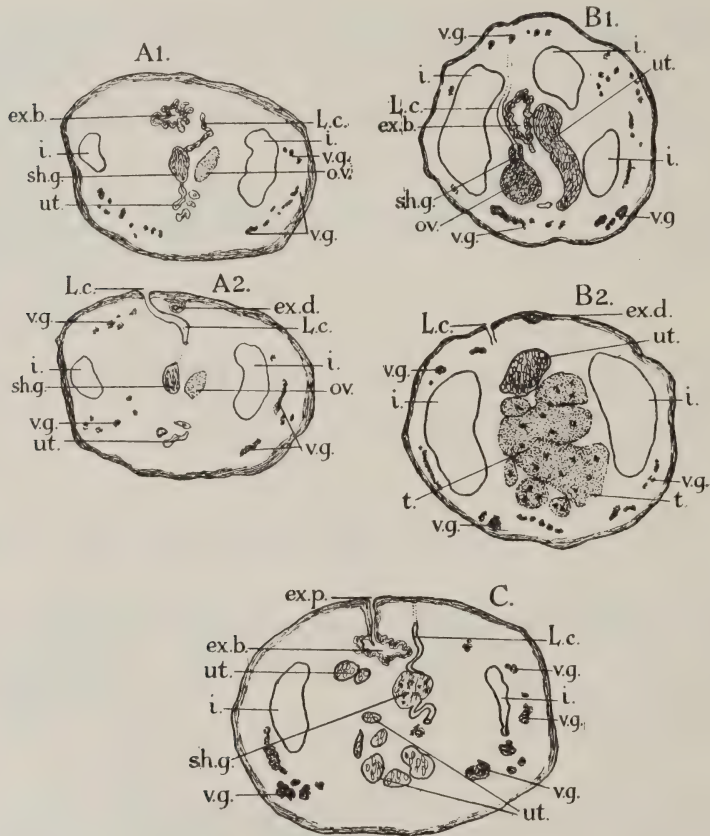


FIG. 1. *Paramphistomum cervi*, transverse sections. *A1* and *A2*—Sections of one specimen at different levels. *B1* and *B2*—Sections of a second specimen at different levels. *C*—Section of a third specimen passing through the excretory pore. *ex.b.*—excretory bladder; *ex.d.*—excretory duct; *ex.p.*—excretory pore; *i.*—intestine; *L.c.*—Laurer's canal; *ov.*—ovary; *sh.g.*—shell gland; *ut.*—uterus; *v.g.*—vitelline gland. $\times 16$.

Careful examination of the descriptions of the six species of *Paramphistomum* in Table IV shows that the differences between them are very minute, and a further comparison of this table with the results of the extensive examination that has been carried out by the writer shows that with one exception all the characters used by Fiscoeder as of specific

value in distinguishing these six species come within the range of what appear to be variations of *P. cervi*. The exception is the length of the pars prostatica; the maximum length observed by the writer for this organ was 594μ , whereas Fiscoeder gives it as 800μ in *P. epiclitum*, and 1.2 mm. in *P. bothriophoron*. But this is such a small difference that the author is inclined to disregard it and to consider it probable that the above species are all one.

There are three species, *P. papilligerum*, *P. papillosum* and *P. indicum*, described by Stiles and Goldberger (1910) which also appear to the writer to be identical with *P. cervi*.

Paramphistomum papilligerum, Stiles and Goldberger, 1910.

Apparently the material on which this species was made consisted of a series of frontal sections loaned to the authors by Shipley.

The only difference between this species and *P. cervi* is that *P. papilligerum* is described as having small papillae on the inner surface of the genital atrium. It has already been shown that papillae in this position may be present or absent in *P. cervi*, and further that the presence of a genital atrium itself is a variable character. There is hence no justification for the separation of this species.

Paramphistomum papillosum, Stiles and Goldberger, 1910.

The material at the disposal of the authors is stated to be a single non-gravid specimen. The species is characterised by the presence of papillae on the anterior end of the worm, in the oral cavity, and in the genital atrium. Papillae in these positions have already been shown to be variable characters of *P. cervi*, being present or absent in one or all of these positions. In *P. papillosum* the excretory pore is stated to be dorsal to the excretory bladder, and in *P. papilligerum* it is stated to be anterior to the bladder; but it must be remembered that in their descriptions of these two worms, Stiles and Goldberger state that eggs were present in the uterus of *P. papilligerum*, and not in *P. papillosum*. It has already been shown that in *P. cervi* the excretory pore appears to pass forward as age advances; this fact is in agreement with the difference observed between the species *P. papilligerum* and *P. papillosum*, when it is remembered that the former is probably a younger specimen than the latter. It is therefore considered that *P. papillosum* is synonymous with *P. cervi*.

Paramphistomum indicum, Stiles and Goldberger, 1910.

These worms were said to have been found in two bottles along with other species, and no eggs were observed. The description and drawings of this species by Stiles and Goldberger agree in all points with many specimens of young *P. cervi* without eggs in the uterus, examined by the writer during the course of the present investigation. That the writer's specimens referred to were young *P. cervi* and not another species is rendered practically certain, because in the same bottles worms in all stages of development could be found, so that the gradual change from worms similar in appearance to *P. indicum* could be followed in a long series until a typical *P. cervi* with uterus full of eggs could be found. The writer is therefore of the opinion that on its present description *P. indicum* cannot be distinguished from young *P. cervi*.

In the writer's opinion *P. gracile*, *P. bothriophoron*, *P. microbothrium*, *P. epiclitum*, *P. bathycotyle*, *P. papilligerum*, *P. papillosum* and *P. indicum* are all synonyms of *P. cervi*.

Paramphistomum liorchis, Fiscoeder, 1901.

This worm is easily distinguished from other species of the genus, because the testes are not lobed ; it is the only species in which the testes exhibit this character, and in which Laurer's canal opens behind the excretory pore.

Paramphistomum pisum, Leiper, 1910.

The material available for examination consisted of two collections, about thirty specimens in all. The location of the parasite in the host (Hippopotamus) is not given, but Leiper (1910) states that it is found in the small intestine.

No gravid specimens were observed by the writer, but about half the material was sexually mature. Leiper says the worms are pisiform when fresh and somewhat contracted when preserved. This agrees with the writer's observations for all of his specimens were slightly contracted with the result that they were almost globular in shape, the largest measuring about 3mm. in diameter. The worms agreed essentially with Leiper's description; both suckers communicate with the exterior by narrow canals as Leiper figures them, but in three specimens which the writer

sectioned the anterior sucker was found immediately beneath the cuticle as in other members of the genus, and is not separated from it by a canal of considerable length as in Leiper's fig. 34.

Paramphistomum gigantocotyle, Brandes, 1896.

Host :—*Hippopotamus amphibius*. Location :—Stomach. Locality :—Africa.

As the original description of this species is somewhat inadequate, Leiper (1910) redescribed it.

According to Leiper this worm may be distinguished from other species by the relative size of the posterior sucker and by the shape of the testes. Although the diameter of the posterior sucker given by Leiper, viz., 3.2 mm. in a worm of 8 mm. in length, is relatively great, it is not by itself a sufficient character for identification, because in *P. explanatum* the relative size of the sucker is often more than this. But the testes appear to be characteristic, as although they are placed one behind the other as in *P. cervi*, they differ in that whilst in the latter they are divided into several lobes, in *P. gigantocotyle* each testis is nearly completely divided into two portions by a deep transverse groove, so that in sections they may appear as four organs, a condition that is never found in *P. cervi*.

Paramphistomum explanatum (Creplin, 1847), Fiscoeder, 1901.

SYNONYMY :—

- Paramphistomum calicophorum*, Fiscoeder, 1901.
- Paramphistomum crassum*, Stiles and Goldberger, 1910.
- Paramphistomum cauliorchis*, Stiles and Goldberger, 1910.
- Paramphistomum fraternum*, Stiles and Goldberger, 1910.
- Paramphistomum siamense*, Stiles and Goldberger, 1910.

The material available consisted of the following collections :—

1. One bottle from the stomach of a bullock killed at Durban, South Africa.
2. One bottle from the stomach of a bullock killed at Townsville, Australia.
(Over 100 specimens.)
3. One bottle from the stomach of a bullock killed at Khartoum, Sudan.
4. One bottle from the stomach of a bullock killed at Blantyre, Nyasaland.
5. Two bottles from the stomachs of two hartebeests shot near Blantyre, Nyasaland. (Both bottles contained over 100 specimens.)

This worm is readily distinguished from *P. cervi*, because the testes are always diagonally situated one overlapping the other, both laterally and antero-posteriorly, in fully grown worms, whereas in full-grown *P. cervi*, the testes lie one directly behind the other.

From this table it is clear that the ratio of the diameter of the sucker to the length of the worm varies above and below Fiscoeder's figure, which closely approximates to the mean. On the whole the sucker is relatively larger than in *P. cervi*, but it is subject to such variations that it cannot be taken as an absolute guide in diagnosis. Another point brought out in the above table is that the sucker is not typically oval in shape, being only occasionally met with in this form.

In describing the genital apparatus, Fiscoeder states :

‘ Auch das genitalatrium ist nur sehr klein. Die dasselbe umgebende, von dem übrigen Körperparenchym wenig abgegrenzte Musculatum ist nur 0.08-0.1 mm. stark, und die in Grunde des Atriums befindliche Papille ist ebenfalls nur äusserst schwach entwickelt.’

Fig. 2 consists of drawings of the genital apparatus of three specimens of *P. explanatum* cut in sagittal section and from these it is clear that such a precise description as the above of this portion of the worm is not permissible. Although this point has not been figured in detail in dealing with other species, the same range of variation in the genital papilla and genital atrium has been found. Fiscoeder says that the genital organs are displaced towards the anterior end of the worm, and that the testes reach near to the ventral surface, in which case they are of necessity in front of the posterior sucker. In some instances this is correct, as is illustrated in fig. 3, but that the testes are not invariably in this position is shown in figs. 4 and 5. In these two worms the testes are seen drawn away from the ventral surface and they lie dorsal to the posterior sucker. In all probability this is an artificial condition brought about by contraction of the worms at the time of fixation, because both these specimens were noted to be considerably contracted before they were cut, and this is borne out by the irregularity of outline shown in the drawings on the dorso-posterior portion of the worm, especially in the case of fig. 4. This probability is further supported by the appearance in fig. 6, which is a sagittal section of an immature well-extended specimen ; in this drawing the single testis figured is seen to be situated nearer to the ventral than to the dorsal surface and well in front of the sucker. The four worms from which the above drawings were made all came from the same bottle, and specimens in varying degrees of contraction and of different ages are found with characters intermediate between them.

If fig. 6 is examined, it will be readily understood how by contraction of the worm the testes are brought to the position seen in the two previous

figures. The base of the posterior sucker slopes backwards and towards the dorsal surface, and antero-posterior contraction of the worm would cause the testes to impinge on this surface, when they would follow the path of

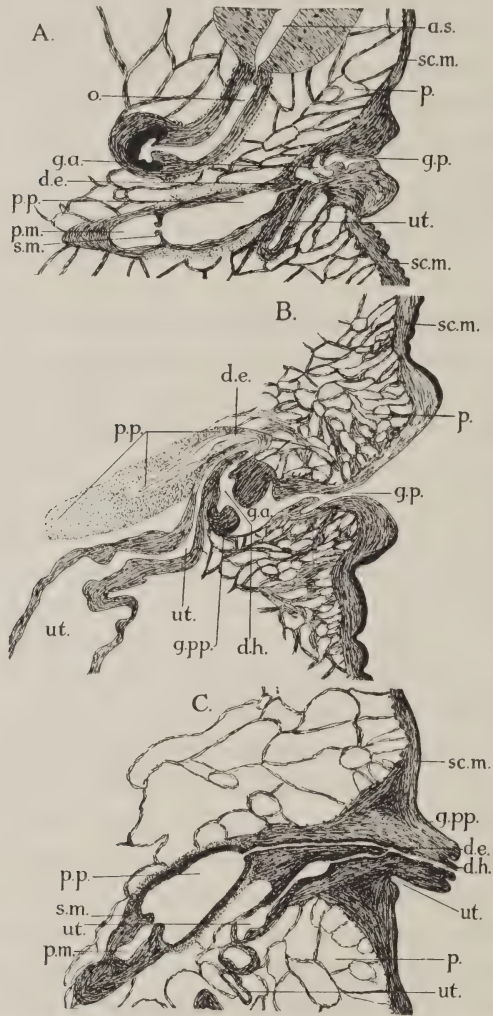


FIG. 2. *Paramphistomum explanatum*. Sagittal section through the genital pore of three specimens. A—Genital papilla fully retracted. B—Genital papilla partly retracted. C—Genital papilla fully extruded. a.s.—anterior sucker; d.e.—ductus ejaculatorius; d.h.—ductus hermaphroditicus; g.a.—genital atrium; g.p.—genital pore; g.pp.—genital papilla; p.—parenchyma; p.m.—pars musculosa; p.p.—pars prostatica; sc.m.—subcuticular muscle; s.m.—sphincter muscle; ut.—uterus. $\times 30$.

least resistance and pass up towards the dorsal surface of the worm; at the same time the testes exert some pressure on the sucker, causing its base to

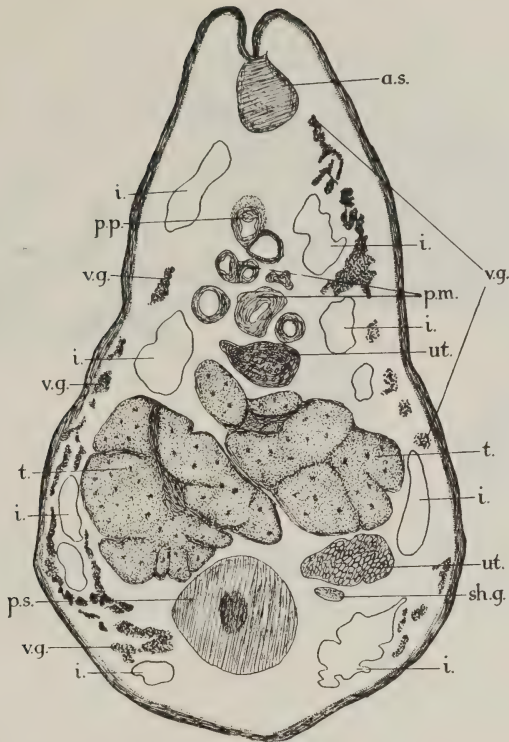


FIG. 3. *Paramphistomum explanatum*. Coronal section of gravid worm. a.s.—anterior sucker; i.—intestine; p.m.—pars muscosa; p.p.—pars prostatica; p.s.—posterior sucker; sh.g.—shell gland; t.—testis; ut.—uterus; v.g.—vitelline gland. $\times 12$.

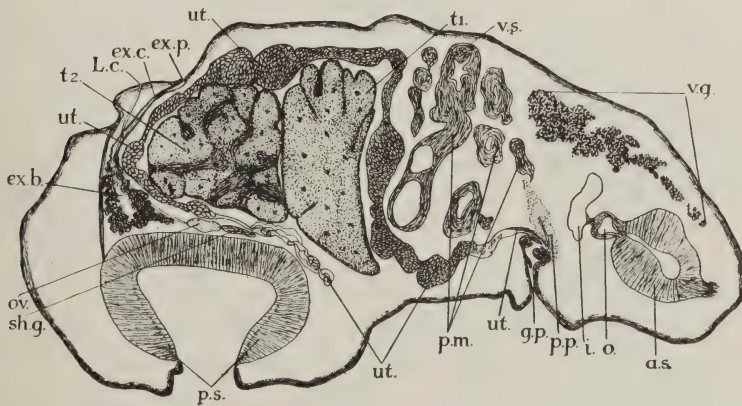


FIG. 4. *Paramphistomum explanatum*. Sagittal section of gravid worm near the mid-line. a.s.—anterior sucker; ex.b.—excretory bladder; ex.c.—excretory canal; ex.p.—excretory pore; g.p.—genital pore; i.—intestine; L.c.—Laurer's canal; o.—oesophagus; ov.—ovary; p.m.—pars muscosa; p.p.—pars prostatica; p.s.—posterior sucker; sh.g.—shell gland; ti.—anterior testis; t2.—posterior testis; ut.—uterus; v.g.—vitelline gland; v.s.—vesicula seminalis. $\times$

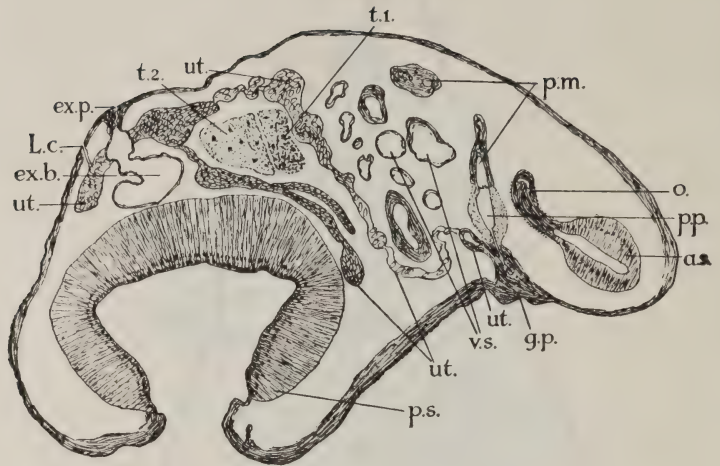


FIG. 5. *Paramphistomum explanatum*. Sagittal section of a partly gravid worm near the mid-line. *a.s.*—anterior sucker; *ex.b.*—excretory bladder; *exp.*—excretory pore; *g.p.*—genital pore; *L.c.*—Laurer's canal; *o.*—oesophagus; *p.m.*—pars musculosa; *p.p.*—pars prostatica; *p.s.*—posterior sucker; *t.1.*—anterior testis; *t.2.*—posterior testis; *ut.*—uterus; *v.s.*—vesicula seminalis. $\times 16$.

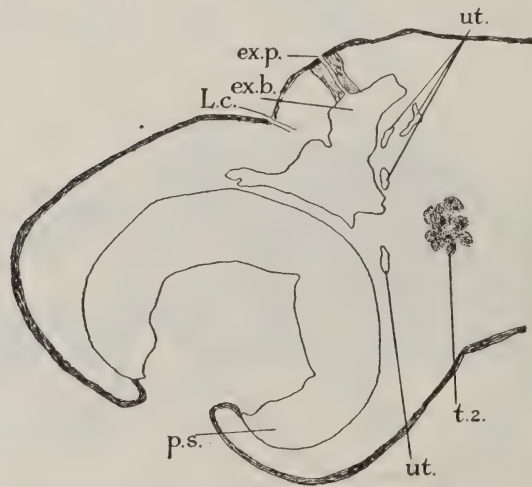


FIG. 6. *Paramphistomum explanatum*. Sagittal section of posterior part of immature worm near the mid-line. *ex.b.*—excretory bladder; *exp.*—excretory pore; *L.c.*—Laurer's canal; *p.s.*—posterior sucker; *t.2.*—posterior testis; *ut.*—uterus. $\times 16$.

become flatter and also making it look almost directly ventrally instead of ventro-posteriorly. The full effect of such contraction is shown in fig. 4.

Fischoeder describes and figures the excretory bladder as being of a long flask-shaped type with a narrow canal running forward from it and opening about the level of the posterior border of the hinder testis. Figs. 4, 5 and 6 clearly show that the shape of the excretory bladder is very variable and that the excretory canal runs dorsally from the bladder in young worms, whereas in older specimens it becomes longer and narrower until, in fully gravid worms, it opens well in front of the bladder.

Stiles and Goldberger (1910), in their diagnostic key of the genus, place *P. explanatum* in the group of worms with the 'excretory pore prevesicular,' and in the sub-group in which the following characters are given as diagnostic. 'Testicular fields median, coincide or overlap, zones lobate, testes much smaller than and near the acetabulum; ventral chamber absent; excretory vesicle long and narrow; acetabulum very large.' Their specific definition is: 'Genital pore in postbifurcal zone; muscosa (?); prostatica longer than muscosa; acetabulum less than half as long as body; caeca sinuous, moderately broad, end in acetabular zone; body 8 to 13 mm. long; type host *Bos indicus* at Berlin, Germany.'

With the exception of the relation of the testes to each other all of the above diagnostic characters are so variable that none of them are reliable.

Paramphistomum calicophorum, Fischoeder, 1901.

At the outset of his description of this worm Fischoeder (1903) states:

'Das Material ist stark geschrumpft, brüchig; trotz Behandlung mit Iod und Wochen langer Einwirkung von Kreosot lässt sich eine zur Untersuchung von Totalpräparaten nur wenig brauchbare Durchsichtigkeit erzielen, mit Ausnahme von einzelnen unreifen Exemplaren aus dem letzt genannten Glase. Dagegen ist es mir gelungen, von reifen Exemplaren aus dem Glase No. F. 659 für meine Zwecke einiger Maassen brauchbare Schnittserien anzufertigen.'

From this it is obvious that he was unable to obtain a dorso-ventral view of a gravid worm, and, from his figures, he was apparently content with sagittal and transverse sections of full-grown specimens; the only dorso-ventral view he gives is that of an immature worm with the testes small and wide apart, an arrangement which is quite unlike that found in gravid specimens. Thus he failed to realise the identical arrangement of the testes in mature *P. explanatum* and *P. calicophorum*.

As the sucker is said to be somewhat smaller in relation to the length

of the worm in *P. calicophorum* than it is in *P. explanatum*, Table VI has been drawn up by utilising the figures given by Fiscoeder for these two worms and by summarising the figures in Table V of the present paper.

TABLE VI.

	<i>P. explanatum</i> , Fiscoeder	<i>P. calicophorum</i>	<i>P. explanatum</i> . Present material summarised from Table V
Length of worm	8 mm. to 13 mm.	10 mm. to 15 mm.	6 mm. to 10·1 mm.
No. of worms measured	?	?	10
Diameter of posterior sucker	3·5 mm. × 3 mm.	3 mm. to 4·3 mm.	2·6 mm. to 3·8 mm.
No. of suckers measured	1	?	10
Ratio of diameter of sucker to length of worm expressed in fractions ...	$\frac{1}{2\cdot3}$	‘Not quite $\frac{1}{3}$ ’	From $\frac{1}{2\cdot9}$ to $\frac{1}{3\cdot6}$

It seems clear from Table VI that there is no constant relation between the diameter of the posterior sucker and the length of the worm.

Fiscoeder recognises the variation to which the genital apparatus is liable and to which attention has been drawn in *P. explanatum* in the present paper. He states :

‘Die Hoden liegen fast neben einander (fig. 29, 30), der vordere etwa in der Mitte des Körpers, mehr dorsal, der hintere mehr ventral (fig. 29, 30 u. 31).’

His references to the figures prove that he is describing the appearance in young worms, which is borne out by his later statement :

‘Bei reifen Individuen nehmen sie die ganze, stark verdickte, hintere Hälfte des Thieres bis dicht zum Saugnapf ein (fig. 31).’

He makes no reference to the appearance of the testes in immature *P. explanatum*.

With regard to the excretory bladder, excretory pore, and Laurer’s canal, he says :

‘In Bezug auf das Lageverhältniss des Excretionporus und der Ausmündungsstelle des Laurer’schen Canals sind häufig gewisse Differenzen zwischen den reifen

und unreifen Individuen zu verzeichnen, die jedoch auch mit der Entwicklung der Hoden und der damit verbundenen stärkern Ausdehnung der hintern Körperpartie in Verbindung gebracht werden können. Während nämlich bei den unreifen Thieren in der Regel die Excretionsblase etwa im Niveau des vordern Randes des Saugnapfes und der Laurer'sche Canal nur 0.3-0.4 mm. dahinter ausmündet (fig. 30, 32 u. Textfig. E), befindet sich der Excretionsporus bei den geschlechtsreifen Thieren meist viel weiter nach vorn, fast in der Höhe des vordern Randes des hintern Hodens (fig. 31), und die Ausmündung des Laurer'schen Canals 0.6-0.8 mm. hinter dem Excretionsporus.'

It is therefore clear that in the case of *P. calicophorum*, Fiscoeder recognised the variation to which these structures are liable, but, as he does not seem to have made a detailed examination of immature material of other species, he failed to realise the general application of this fact. While in agreement with Fiscoeder in the first part of his statement, viz., that the excretory pore and excretory canal vary in their relations to the bladder as age advances, the writer cannot support the latter part of his statement that Laurer's canal opens further behind the excretory pore in gravid worms than it does in immature examples. While agreeing that a variation in this particular can be found, it has been observed to be quite independent of age.

Stiles and Goldberger (1910), apparently basing their definition of *P. calicophorum* on Fiscoeder's paper (1903), write :

'Excretory pore prevesicular.

Testicular fields separate, not median, zones overlap, testes lobate, much smaller than acetabulum ; . . . excretory vesicle not narrow but swollen . . .'

From this it is clear they have ignored Fiscoeder's statements quoted above and have taken their definition mainly from characters found in immature worms, which makes it useless for diagnostic purposes. Careful comparison of Fiscoeder's descriptions of the species *P. explanatum* and *P. calicophorum* thus indicates that there are no differences between them, except such as may be explained by differences in age and normal variation ; therefore *P. calicophorum* is a synonym of the species *P. explanatum*.

Paramphistomum crassum, Stiles and Goldberger, 1910.

Stiles and Goldberger (1910) made the species *P. crassum* from three specimens which they state were found with other forms in a bottle from India, the host being *Bos indicus*. They also say that no eggs were seen, so it is probable their material was immature.

On comparing Stiles and Goldberger's description of *P. crassum* with

Fischoeder's description of *P. calicophorum*, the only essential difference between the two is that the excretory pore is dorsal to the excretory bladder in *P. crassum*, and although Stiles and Goldberger assert that the excretory pore is anterior to the excretory bladder in *P. calicophorum*, it is not in agreement with Fischoeder's statement, quoted above, except in fully grown worms, and with this the writer's observations are in agreement. It has also been shown that in *P. explanatum* without eggs the excretory pore is in the position ascribed to it in *P. crassum* by Stiles and Goldberger. When it is recalled that the latter observers saw no eggs it seems probable that they were dealing with young specimens of the same species as Fischoeder.

Paramphistomum cauliorchis, Stiles and Goldberger, 1910.

In describing this species Stiles and Goldberger (1910) state that they found three specimens in one bottle and four in another. The host was *Bos indicus* and eggs were not observed. In their description of *P. crassum* Stiles and Goldberger say that it closely resembles *P. cauliorchis*; this is fully borne out by comparing the two descriptions. There is this difference, however, viz., that in *P. cauliorchis* they state that Laurer's canal 'opens slightly to right or left of the median line, 60 to 320 μ cephalad of the excretory pore,' whereas in *P. crassum* Laurer's canal is described as opening 'about 0.72 mm. caudad of the excretory pore.' But there is some doubt as to the correctness of their observations in *P. cauliorchis* for two reasons. First, in their fig. 62, which is a side view of *P. cauliorchis*, they show Laurer's canal running parallel with the excretory canal, and although the termination of Laurer's canal is not actually shown, it looks as if it would open about the same level as the excretory pore. In the second place, they have made a subgenus *Cauliorchis* of which *P. cauliorchis* is the type, and in their definition of this Stiles and Goldberger state that Laurer's canal is 'caudad to caudo-laterad of the excretory pore, the two pores may be close together . . .' Another point is that in *P. crassum* the testicular fields are said to overlap and in *P. cauliorchis* they are said to be separate, in the latter case being similar to their definition of *P. calicophorum*. The writer has already shown, and is confirmed by Fischoeder, that in *P. explanatum* the testes are separate in young worms, and that in older ones the fields overlap, and although age is the most important factor in influencing this difference, the writer has found young worms of the same

type with the testes overlapping. It is accordingly concluded that there is no difference between *P. crassum* and *P. cauliorchis*.

Paramphistomum fraternum, Stiles and Goldberger, 1910.

Railliet, Henry and Bauche (1914a) state that *P. fraternum* is a synonym of *P. explanatum*, and they advance such good reasons for their opinion that it is proposed to accept their conclusion without further discussion. In the light of the present investigation, however, there is one point of interest in the conclusion of Railliet, Henry and Bauche, viz. : Stiles and Goldberger give as one of the distinguishing characters of *P. fraternum* that the genital pore is opposite the anterior sucker in this species, whereas it is posterior to the gut fork in *P. explanatum*. From this it may be inferred that the above observers do not consider the position of the genital pore of any specific value. Moreover, Fiscoeder also seems to be of the same opinion, as Railliet, Henry and Bauche state that they obtained his opinion on their material and that he agreed with them as to its identity.

Paramphistomum siamense, Stiles and Goldberger, 1910.

This species is differentiated from *P. cervi* and *P. fraternum* by Stiles and Goldberger and is therefore considered new by them. In their diagnosis from *P. cervi* they use the difference in size of the posterior sucker, the position of the genital pore, and the shape of the worm, but they omit the one real distinguishing character, viz., the different relations of the testes to one another in the two species. *P. fraternum* is distinguished from *P. siamense* because the worms are said to be of different shape ; the posterior sucker of *P. fraternum* is relatively smaller than it is in *P. siamense* ; and the genital pore is proportionately nearer to the anterior end in *P. fraternum*. The question of small differences in shape may be disposed of by reference to Plate VI, fig. A, which is a photograph of several specimens of *P. explanatum*, all of which were taken from one bottle. With regard to the position of the genital pore, this is given as midway between that described for *P. explanatum* and *P. fraternum*, so the opinion of Railliet, Henry and Bauche (1914a), which has been quoted under the discussion of the latter species, is of equal value in this case. The relative difference in size of the posterior sucker in the two species requires more careful consideration.

In the case of *P. fraternum* Stiles and Goldberger say that only two specimens 'in poor condition' were available. The length of one of these specimens is given as 9.75 mm. when in alcohol, and the same worm measured 8.94 mm. after imbedding and sectioning. The diameter of the posterior sucker of this worm is given as 3.75 mm. in the antero-posterior and 3.25 mm. in the transverse direction. In the case of *P. siamense* the length of two specimens measured in glycerine alcohol is given as about 6 mm. and 9 mm. respectively. The posterior sucker was measured in three 'press preparations,' and the diameters of the three are given as 3.5 mm., 4 mm. and 5 mm. respectively. It is not quite clear what is meant by press preparations, but it is assumed that it means that the worms were subject to pressure before being measured. The writer has found that pressure between slides is of great advantage in obtaining a clear view of the internal organs in carbolic cleared specimens, but it was found that measurements of worms while under pressure in this way were quite unreliable. This was especially the case with regard to the posterior sucker; because, the worms being much thicker at the posterior end than at the anterior end, when pressure was applied a considerable flattening and consequent distortion was caused to the hinder end before the anterior end was subject to any pressure. It is therefore clear that the posterior portions of the worms were always relatively more distorted than the anterior portions, and hence the structures in the hinder part were relatively greatly increased. It seems that this is what has occurred in Stiles and Goldberger's case, and that owing to their failure to recognise this fact they have been led to ascribe specific value to what is in reality an artificial condition. Indeed, from the writer's experience, it is surprising that the difference in size of the posterior sucker in *P. fraternum* and *P. siamense* was not greater than they actually found it. It is therefore considered that the small difference between the relative size of the posterior suckers in these two worms should not be regarded as of any diagnostic value, and in consequence the two worms are probably identical with one another and with *P. explanatum*.

As a result of the above investigation it is concluded that *P. calicophorum*, *P. crassum*, *P. cauliorchis*, *P. fraternum* and *P. siamense* are all synonyms of *P. explanatum*.

In all the species of the genus *Paramphistomum* that have been dealt with up to the present the excretory pore is anterior to the opening of

Laurer's canal. Those species in which Laurer's canal opens anterior to the excretory pore will now be considered. As the writer has not had an opportunity of examining the following species, the description is in each case summarised from the original.*

Paramphistomum orthocoelium, Fiscoeder, 1901.

SYNONYMY :—

Paramphistomum dicranocoelium, Fiscoeder, 1901.

Paramphistomum streptocoelium, Fiscoeder, 1901.

Paramphistomum scolicoelium, Fiscoeder, 1904.

Paramphistomum parvipapillatum, Stiles and Goldberger, 1910.

Paramphistomum shibleyi, Stiles and Goldberger, 1910.

First found in the stomach of a *Bos kerabau* that died in Berlin.

The following notes were made from Fiscoeder (1903).

Cuticular papillae are present on the anterior end of the worm. The oesophagus is twice as long as the anterior sucker, and is surrounded by especially large and numerous cells. The muscle walls of the oesophagus are not thicker than in most other species of the genus. The gut caeca are not wavy, they are almost straight; they lie about midway between the dorsal and ventral surfaces on each side of the worm, and they end 0.5 mm. to 1 mm. in front of the posterior sucker; the diameter of the caeca is 1 mm. to 1.2 mm. dorso-ventrally and 500μ to 600μ transversely. With the exception of the vitellaria, the genital organs exhibit no special characters. The genital papilla is well developed and almost fills the atrium, being in most cases slightly protruded. The testes lie one behind the other in the posterior half of the worm; their size and the distinctness of their lobulation is variable. The vitellaria, however, consist of round to oval groups of follicles nearly uniform in size and about 300μ in diameter. As a rule, they are in a single row along the ventral border of the caeca on each side except near the posterior end, where they are grouped to the number of from four to six follicle groups which lie close together. The eggs are 105μ to 115μ in length by 60μ to 65μ in breadth.

* Since completion of this paper the writer has been able to examine a collection of a few specimens of *P. orthocoelium* from the stomach of a sheep at Hong Kong. Although it is necessary to section the worm to see the course of Laurer's canal, simple clearing in carbolic acid is sufficient to establish the identity of this species. It is easily distinguished from *P. cervi* by the vitellaria which in this species are arranged in very numerous comparatively small groups of follicles, never more than about 300μ in diameter, and showing a marked tendency to encroach on the dorsal and ventral surfaces of the worm, whereas in *P. orthocoelium* the number of follicle groups is much less, they are considerably larger, being up to 700μ in diameter, and are limited almost exclusively to the lateral fields external to the gut caeca.

Paramphistomum dicranocoelium, Fiscoeder, 1901.

The following notes are taken from Fiscoeder (1903).

Cuticular papillae were not seen on the anterior end. The worm is very near *P. orthocoelium*. The oesophagus is shorter than in *P. orthocoelium*, its extreme length being one and a half times as long as the anterior sucker, and instead of becoming thicker only quite close to the gut fork the muscle wall commences to thicken about its middle, and from this point it gradually increases from 20μ to 60μ - 75μ at the posterior end. The gut caeca are straight, but differ from *P. orthocoelium* in being nearer to the dorsal than to the ventral surface, and they are only 250μ to 350μ in diameter; they end about 1 mm. in front of the posterior sucker. The genital papilla is well developed, but is strongly retracted as a rule. The vesicula seminalis is larger and lies farther towards the dorsal surface, but on the other hand the pars muscosa is not so long as it is in *P. orthocoelium*, and the pars prostatica is somewhat shorter also. The ductus hermaphroditicus may be a fairly broad pear-shaped cavity, or, when the papilla is strongly retracted, the ductus hermaphroditicus may be merged in the genital atrium. The vitelline glands are arranged in similar groups to *P. orthocoelium*, but they lie as a rule in two rows and show no special grouping behind the ends of the caeca. The anterior ends of the vitellaria may be at different levels. The other genital organs are approximately the same as in *P. orthocoelium*. The eggs measure 145μ to 150μ in length and 75μ to 80μ in breadth.

Paramphistomum streptocoelium, Fiscoeder, 1901.

The following notes were taken from Fiscoeder (1903).

Cuticular papillae are present on the anterior end as in the case of *P. orthocoelium*. The oesophagus is only about as long as the anterior sucker; the gut caeca are strongly convoluted and end opposite the base of the sucker. The genital atrium is distinguished by the presence of a ring-like prominence on its inner wall which divides the atrium into a small ventral and a large dorsal chamber. The testes, as well as varying in proportion to the size of the worm, may be of different sizes in the same worm and apparent partial atrophy of these organs has been noted in gravid worms. The position of the testes is the same as in *P. dicranocoelium*. The female genitalia only show slight differences from the previous species.

The vitellaria are confined to the sides of the worm and stretch from the gut fork in front to the posterior sucker behind as in *P. dicranocoelium*. The follicles are in groups similar to the previous species (300μ to 700μ in diameter), but they are present in larger numbers and are therefore smaller in size than in the two previously named species. The anterior limits of the vitellaria may be at different levels on the two sides as in *P. dicranocoelium*. The eggs measure 105μ to 115μ in length by 60μ to 65μ in breadth.

Paramphistomum scoliocoelium, Fiscoeder, 1904.

The following notes are taken from Fiscoeder (1904).

The musculature of the oesophagus is similar to that of *P. dicranocoelium*. The gut caeca are less wavy than in *P. streptocoelium*, and they are nearer to the dorsal than the ventral surface as in *P. dicranocoelium*. The genital pore is, as a rule, widely open. The vitellaria are similar to the other three species; they are composed of coarse follicles which lie at the sides of and external to the gut fork, from about the level of the gut fork in front opposite to the base of the posterior sucker behind. The eggs are 135μ to 145μ in length by 65μ to 75μ in breadth.

Paramphistomum parvipapillatum, Stiles and Goldberger, 1910.

The following notes are taken from Stiles and Goldberger (1910).

The cavity of the anterior sucker is furnished with moderate sized papillae. The oesophagus is estimated to be not shorter than the anterior sucker and it exhibits a thickening of its muscle wall in its posterior half. The gut caeca are slightly wavy and end opposite the middle of the posterior sucker. The genital papilla is embraced by a ring-like collar beset with fine papillae. External to this collar is another ring marked off from it by a groove, and this groove may not be present in cases with the genital papilla protruded. The vitellaria consist of numerous follicles lying at the sides of, above, and below the gut caeca; the gland groups on the left-hand side extend slightly further inwards than those on the right hand. The vitellaria extend from the hinder end of the anterior sucker in front to opposite about the middle of the posterior sucker behind. The eggs measure 135μ in length by 67μ in diameter.

Paramphistomum shipleyi, Stiles and Goldberger, 1910.

The following notes are from Stiles and Goldberger (1910).

The entrance to the anterior sucker and the sucker itself are lined with small papillae. The muscle wall of the oesophagus begins to grow thicker from about the middle of its length towards the posterior end. The caeca are wavy and end about the level of the anterior border of the cavity of the posterior sucker. The diameter of the gut varies at different points along its course, there being marked dilatations followed by constrictions. The testes are one behind the other, but overlap slightly. The ductus ejaculatorius opens close to, but separate from and just above the opening of the uterus. The space into which this ductus ejaculatorius opens is narrow and slit-like.

'From this space a short duct passes ventrad and may be regarded as piercing the axial region of a mushroom-like structure (figs. 123-126) to open into another slit-like atrium somewhat larger, however, than the one into which the male and female ducts open. A duct about 30μ in diameter leads from this atrium and apparently pierces a stout conical papilla, which may be regarded as the genital papilla, to open into a small genital atrium which connects with the exterior by the genital pore.'

The eggs are about 135μ in length by 71μ in breadth.

In conducting a critical examination into the specific value of the above worms, it is in the first place obvious that the points used for differentiation are all similar to those used in the group of worms that have been considered under *P. cervi*. But in the present instance the differences are even smaller than in the former case. For instance, differences in length of the oesophagus greater than in these six species have been noted in all species examined. This is only to be expected when it is realised that the oesophagus is well supplied with muscle, contraction or relaxation of which can easily account for the differences observed. The amount of increase of thickness towards the posterior end of this organ has also been shown to vary considerably in the same species. The point of termination of the gut caeca only varies very slightly in the above six species; this character has been found to have no diagnostic value in other cases, and that in the present instance it is equally valueless is appreciated, when it is noticed that in *P. scoliocoelium*, Fiscoeder shows the caeca ending in front of the posterior sucker in fig. 7, and behind the anterior border of the sucker in fig. 8, although in the text he says they end in front of the posterior sucker. It has also been found that slight differences in the

amount of convolution of the caeca, as well as in their diameter, are of no value. A moment's reflection will explain the reason for this. The caeca are hollow structures furnished with muscular walls and it will thus be obvious that the amount of convolution may vary considerably according to the degree of contraction of the muscular wall of the gut and of the whole worm. The value of slight differences in the distribution of the vitellaria has also been shown of no use for specific diagnosis in all other species, and that the same probably applies in the present series of worms is borne out by comparison of the statements in regard to these glands in several of the worms. For example, Fiscoeder states that *as a rule* the gland groups are in a single row in *P. orthocoelium*, and in *P. dicranocoelium* they are *as a rule* arranged in a double row; but as he does not state what the exceptions to these rules are, all that one can infer is that the vitellaria are subject to some variation in both these species and cannot, therefore, be accorded any specific value. The liability to variation of the vitellaria is also borne out by the following contradictory statements by the same author: in *P. orthocoelium* he says the vitelline follicles are in groups, each of which is about 300μ in diameter; in *P. dicranocoelium* they are similar to the above; and in *P. streptocoelium* they are in groups similar to the above, but having a diameter of from 300μ to 700μ ; whilst in the next sentence he states they are present in *P. streptocoelium* in far greater numbers than in the two previous species and are in consequence of smaller size. With regard to the genital apparatus, there is no evidence of any allowance having been made for variations due to protrusion or retraction of the genital papilla at the time of fixation. For example, the genital papilla of *P. orthocoelium* is described as being well developed and in most cases filling the atrium; in *P. dicranocoelium* the papilla is said to be well developed and in most cases strongly retracted; in *P. streptocoelium* a ring-like prominence divides the atrium into two chambers; in *P. scoliocoelium* the genital pore is stated to be, as a rule, widely open; in *P. parvipapillatum*, the papilla is described as being embraced by a collar-like ring beset with minute papillae; and in *P. shipleyi* from the single sectioned example that they studied Stiles and Goldberger describe a complicated arrangement of ducts and atria which, in the writer's opinion, is only a description of a worm with the papilla in strong retraction such as can be found in any species, if enough specimens are examined. All the various descriptions of genital papilla and atrium described above have been seen by the writer in all the species in which he has had sufficient

material to examine a long series of mature worms. It is therefore considered that in the present case they cannot be regarded as specific differences. The only other point relates to the small papillae described as present in some species of this group of worms and absent in others. In all other species they have been found to vary to a great extent, and accordingly it is probable that in the present case they vary in the same way, and are in consequence of no diagnostic value.

The evidence obtained from the examination of closely allied species, indicates that the points on which the differentiation of the above six species is based, are of no specific value. It is therefore considered that *P. dicranocoelium*, *P. streptocoelium*, *P. scoliocoelium*, *P. parvipapillatum* and *P. shipleyi* are synonyms of *P. orthocoelium*.

Paramphistomum buxifrons, Leiper, 1910.

Host :—*Hippopotamus* sp. Location :—Stomach. Locality :—Uganda.

According to Leiper, *P. buxifrons* can readily be distinguished by its leaf-like shape which resembles the leaf of a box tree. A large example may measure 5 mm. in length by 3 mm. in breadth and be only 0.4 mm. in thickness at the middle of the body. The testes also are a distinguishing character, as they are not lobed and they are placed diagonally in the posterior part of the worm. The only other species with testes not lobed are *P. liorchis* and *P. wagandi* and in these cases the testes are one behind the other, but in *P. buxifrons*, Laurer's canal opens in front of the excretory pore, whilst in *P. liorchis* Laurer's canal is behind the excretory pore.

Paramphistomum wagandi, Leiper, 1910.

Host :—*Hippopotamus* sp. Location :—Stomach. Locality :—Uganda.

The testes are not lobed and are placed one behind the other, and the worm is therefore very similar to *P. liorchis*; the two species are distinguished by the position of the opening of Laurer's canal, which is in front of the excretory pore in *P. wagandi*, whereas it is behind the excretory pore in *P. liorchis*.

In his descriptions of these species, Leiper lays down by definite measurement the exact size and position of the various organs, the appearance of the genital atrium, the shape of the excretory bladder, etc. In most cases these particulars appear to have been obtained from a single sectioned

specimen. This fact is considered unfortunate, because slight variations from the data given by Leiper are almost certain to be found when these worms are more fully known, and will in all probability lead to a multiplication of species on the ground of slight variations, in the same way as seems to have occurred in most of the other species.

Genus *Cotylophoron*, Stiles and Goldberger, 1910.

Definition.—*Paramphistominae*: with a genital sucker distinctly marked off from the subcuticular muscle layer.

Type species: *Cotylophoron cotylophorum* (Fischöder, 1901), Stiles and Goldberger, 1910.

KEY TO SPECIES

Laurer's canal opens posterior to excretory pore	<i>C. cotylophorum</i>
Laurer's canal opens anterior to excretory pore	<i>C. minutum</i>

Cotylophoron cotylophorum (Fischöder, 1901), Stiles and Goldberger, 1910.

SYNONYMY:—

Paramphistomum cotylophorum, Fischöder, 1901.

Cotylophoron indicum, Stiles and Goldberger, 1910.

First found in the stomach and intestines of *Bos* sp. in German East Africa.

The material available for study in the present case consisted of the following collections:—

1. Ten bottles from the stomach of bullocks killed at Sierra Leone, West Africa.
2. Four bottles from the stomach of buffaloes (*Bubalus* sp.) in the Upper Shire River, Nyasaland.
3. Four bottles from the stomach of two nswala (*Aepyceros melampus*) shot in the Upper Shire River District, Nyasaland.
4. One bottle from the stomach of a Pagan dwarf bull from Ilorin, Northern Nigeria.
5. One bottle from the stomach of a waterbuck (*Cobus* sp.) from Zeref, Khartoum.
6. One bottle from the stomach of a hartebeest (*Bubalis* sp.) from Nyasaland.
7. One bottle from the stomach of an antelope sp. (?) from Rhodesia.
8. One bottle from the stomach of an antelope sp. (?) from Nyasaland.

In some of these bottles were many hundreds of specimens, so ample material was available for examination.

The species *C. indicum* was made by Stiles and Goldberger from six specimens. They state that no eggs were observed, so it is probable that their material was immature.

The differences between *C. cotylophorum* and *C. indicum* are summarised by Stiles and Goldberger as follows :—

‘*Cotylophoron indicum* comes close to *C. cotylophorum* from which it differs chiefly in the structure of the oesophagus, which is provided with a bulbous thickening in the latter species, but is without it in the former. The two differ also in the details of structure of the copulatory apparatus and in the position of the genital pore. In *C. indicum* the genital sucker is less sharply delimited, projects less, has a much smaller genital atrium, and the genital pore is decidedly postbifurcal; on the other hand, in *C. cotylophorum* the genital sucker is sharply marked, with rim prominently bulging the venter, with a relatively roomy genital atrium and with the genital pore in the bifurcal zone.’

It should be noted that Fiscoeder (1903) in his description of *P. cotylophorum* says the uterus is strongly convoluted and it is full of eggs, showing that his specimens were mature.

The following points have been worked out from the examination of many specimens of *C. cotylophorum*, either cut and mounted in serial sections, or examined whole in carbolic acid.

Oesophagus. In their description of the species *C. indicum*, Stiles and Goldberger state that the walls of the oesophagus are thick, but give no other important details of its characters. In the present instance, the thickness of the muscle walls of the oesophagus, as well as its length and direction, were found to be very variable. Although it was much more distinct in some cases than in others, there was always a gradual increase in thickness of the muscle wall of the oesophagus from the anterior end towards the posterior end, in exactly the same way as described in *P. cervi*. Fig. 7 represents camera lucida drawings of eleven specimens of *C. cotylophorum* cut in sagittal section. It will be noted that in figs. K and A, the oesophagus is approximately the same as in fig. 45 by Stiles and Goldberger, which is a drawing of *C. indicum*. Now, taking the remaining drawings in fig. 7 in the following order D, B, E, C, L, F, G, H, it will be observed that as the oesophagus gradually increases in length, its posterior extremity becomes more and more bulbous. Drawings C, L, G, and F are very similar to Fiscoeder’s fig. 38, which is a drawing of *C. cotylophorum* cut in the sagittal plane. In addition to the above characters it was noted that the worms from which drawings J and K were made contained no eggs, whilst all the others had eggs in the uterus, those with the longest oesophagus having the most eggs. It seems probable, therefore, that the differences in the oesophagus in *C. indicum* and *C. cotylophorum* are really due to differences of age. This is all the more likely when it is remembered that Stiles and Goldberger’s material did not contain eggs,

and that Fiscoeder's did. Two other points are also well illustrated in the above series of drawings, viz., that the course and length of the oesophagus are subject to considerable variation, and that the position of the genital pore varies in relation to the gut fork to such an extent that neither of these points is reliable for distinguishing between *C. indicum* and *C. cotylophorum*.

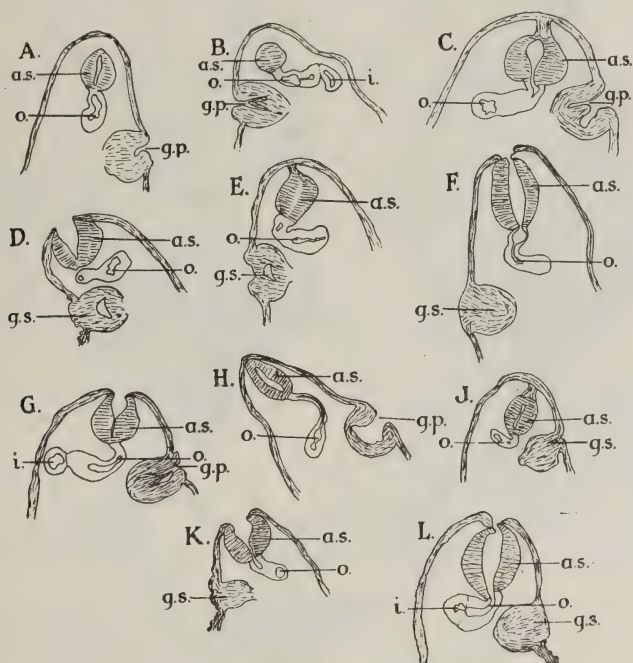


FIG. 7. *Cotylophoron cotylophorum*. Sagittal section through the anterior ends of eleven specimens to show oesophagus and genital sucker. a.s.—anterior sucker; g.p.—genital pore; g.s.—genital sucker; i.—intestine; o.—oesophagus. $\times 12$.

Genital apparatus. The differences in size, and degree of extrusion or retraction of the genital sucker and papilla, with consequent changes in the genital atrium, were almost as numerous as the specimens examined. This is well illustrated in figs. 8 and 9, which show such great differences in appearance that at first sight it might be considered that different species are being dealt with, but it should be borne in mind that the above examples have been chosen for this very reason, and that many specimens have been examined showing all possible intermediate stages, thus rendering it practically certain that it is only a question of individual variation. Fig. 8, A1 and A2, are two sections of the same worm, and they have been included because Fiscoeder (1903) states that the male and female

openings have always been noted by him to be separate in *C. cotylophorum* as shown in fig. 8, A2, which closely corresponds to Fiscoeder's fig. 38. But a later section (fig. 8, A1) showed the male and female ducts uniting within the substance of the genital papilla and opening on the surface by

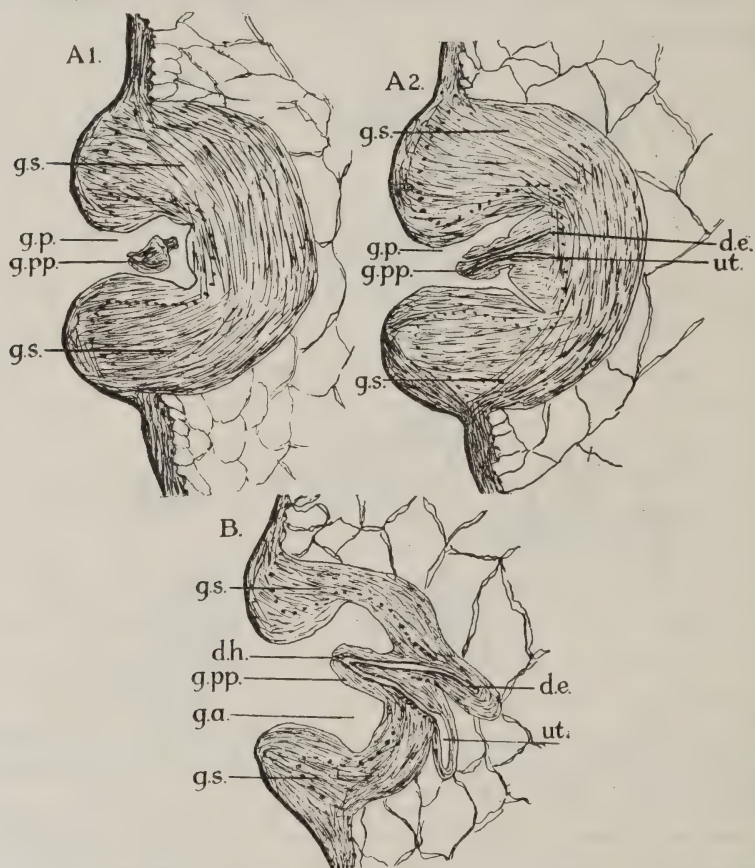


FIG. 8. *Cotylophoron cotylophorum*. Sagittal section through genital sucker. A1—Section showing tip of genital papilla with male and female ducts uniting in the usual way. A2—Section of same specimen with male and female ducts apparently opening separately, because tip of genital papilla is not seen. B—Section of another specimen with genital papilla lying in a wide atrium. d.e.—ductus ejaculatorius; d.h.—ductus hermaphroditicus; g.a.—genital atrium; g.p.—genital pore; g.pp.—genital papilla; g.s.—genital sucker; ut.—uterus. $\times 45$.

a common duct. It is therefore clear that there is no essential difference between this worm and other species with regard to the termination of the male and female ducts. Fig. 8, B, shows how different the genital pore may appear if it is relaxed with a large genital atrium and a patulous genital pore, but in sections not passing through the genital atrium the genital

sucker was seen to be just as thick as in other cases. In fig. 9 two very different appearances of the genital apparatus are shown. Fig. 9, A, shows the whole genital sucker protruded beyond the surface of the worm, while in 9, B, it is deeply retracted within the body. It will be noted that in fig. 9, A, the subcuticular muscle extends past the base of the genital sucker in an apparently unbroken column of fibres, and that even opposite its base the parenchyma is not sharply marked off from the sucker, whereas in fig. 9, B, with the sucker deeply retracted, this separation is quite distinct. The conclusions drawn from these two figures are that the demarcation of

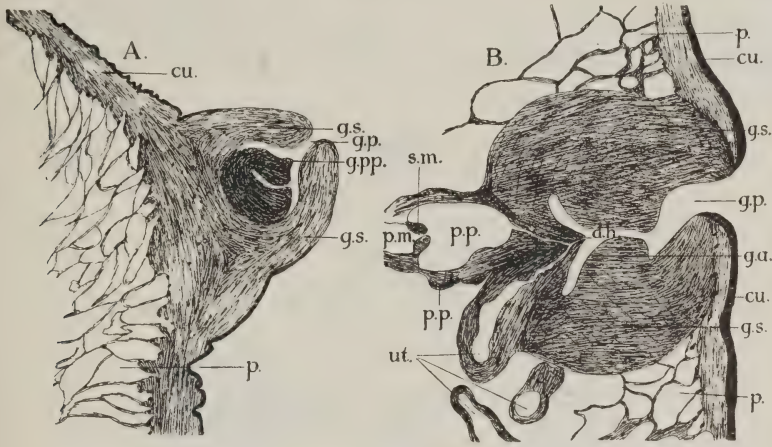


FIG. 9. *Cotylophoron cotylophorum*. Sagittal section of genital sucker of two specimens. A—Genital sucker fully extruded. $\times 40$. B—Genital sucker fully retracted $\times 60$. cu.—cuticle; d.b.—ductus hermaphroditicus; g.a.—genital atrium; g.p.—genital pore; g.pp.—genital papilla; g.s.—genital sucker; p.—parenchyma; p.m.—pars muscosa; p.p.—pars prostatica; s.m.—sphincter muscle; ut.—uterus.

the sucker from the parenchyma in this genus is more apparent than real, and that it is probably brought about by the subcuticular muscle and the contiguous parenchyma being stretched around the sucker when it is in the retracted condition. Comparison of the shape and size of the atrium in the drawings will make it sufficiently clear without further comment that minute descriptions of the shape and number of chambers in this atrium cannot be regarded as of any value for specific diagnosis. The conclusion arrived at from consideration of the above facts is that Stiles and Goldberger, in describing *C. indicum* from six specimens with no eggs in the uterus, were in all probability dealing with immature specimens of *C. cotylophorum*.

In addition to the above points, which were worked out in sectioned

specimens, evidence of variation in other characters was obtained by the examination of eighty specimens cleared in carbolic acid and examined whole.

Gut caeca. The amount of convolution of the caeca varies considerably, as does their point of termination. The most usual position for the caeca to end in this species is about opposite the middle of the posterior sucker, but in some cases they both ended well in front of the anterior border of the posterior sucker, and in others they nearly reached the posterior border of the posterior sucker. Between these two extremes all intermediate stages were found, and in a few instances the caeca on the two sides of the same worm ended at different levels. As a rule, the final turn of the caeca was directed dorsally, but this was by no means invariable, as is clearly shown in fig. 10.

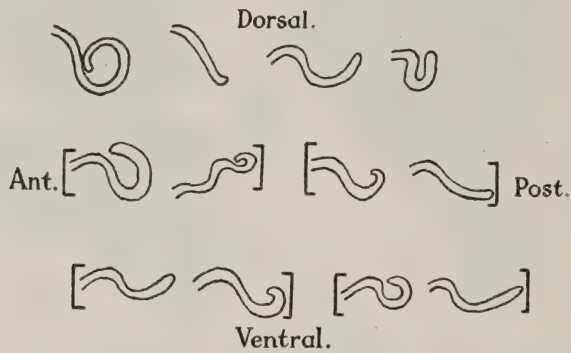


FIG. 10. *Cotylophoron cotylophorum*. Drawings showing various forms of termination of gut caeca. These figures are not to scale, and are drawn from carbolic cleared specimens. Those in brackets are the two caeca from a single worm.

Vitellaria. The distribution of the vitelline glands and the number of collections of follicles in each gland showed a remarkable degree of variation. The glands commenced anteriorly anywhere from about opposite the middle of the anterior sucker to a point slightly behind the genital pore; as a rule, they extended posteriorly to a little behind the termination of the gut caeca, but in a few instances groups of follicles were seen extending to the extreme posterior end of the worm and surrounding the opening of the posterior sucker in the same way as in all the other species examined. The degree of extension inwards on the dorsal and ventral surfaces varied in the same way as in *P. cervi*. The anterior extension of the gland was often different on the two sides, and in one extreme instance the vitelline gland on the left side began in front of the genital pore and ended just

behind the corresponding caecum, but on the other side the gland was composed of a closely packed collection of follicle groups, which commenced opposite about the middle of the hinder testis and ended opposite the middle of the posterior sucker, being completely confined to the outer side of the caecum of that side.

Excretory system. The change in the relations of the excretory pore to the excretory bladder in worms of different age, which has been referred to in *P. cervi* and *P. explanatum*, has been found to hold good in the case of *C. cotylophorum*. This is clearly shown in fig. 11, which represents the

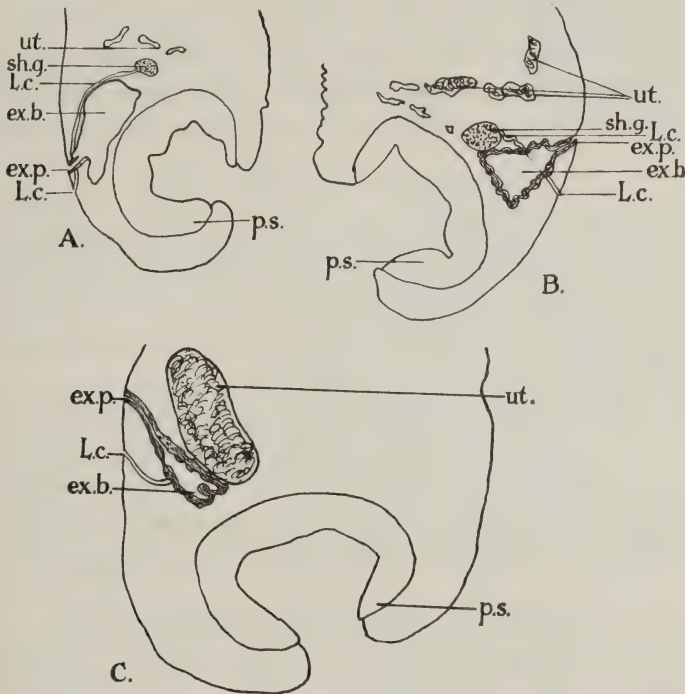


FIG. 11. *Cotylophoron cotylophorum*. Sagittal sections of three specimens near the mid-line to show the alteration in course of the excretory canal with increasing age. A—Immature worm. B—Partly gravid worm. C—More fully gravid worm. *ex.b.*—excretory bladder; *exp.*—excretory pore; *L.c.*—Laurer's canal; *p.s.*—posterior sucker; *sh.g.*—shell gland; *ut.*—uterus $\times 18$.

posterior ends of three specimens of *C. cotylophorum* of different ages. These figures also emphasise the fact that the shape of the excretory bladder is very variable.

Leiper (1910) described two worms from the hippopotamus, which he placed in the genus *Paramphistomum*, but both of them have a definitely

delimited muscular thickening round the genital pore. Following the classification of Stiles and Goldberger (1910) these worms should be placed in the genus *Cotylophoron*. The following are the principal distinguishing features of these species according to Leiper's descriptions.

Cotylophoron minutum (Leiper, 1910).

SYNONYMY :—*Cotylophoron sellsi* (Leiper, 1910).

First found in the stomach of a *Hippopotamus* sp. in Uganda.

The testes are small and oval in shape and they lie one behind the other, being separated by a space about equal to the diameter of a single testis. Although it is not stated in the text, it is assumed from Leiper's fig. 32 that the testes are not lobed. Laurer's canal opens in front of the excretory pore. This worm differs from *C. cotylophorum* in that the testes are not lobed and that Laurer's canal opens in front of the excretory pore.

Cotylophoron sellsi (Leiper, 1910).

This species is very similar to *C. minutum*, the only differences being that it is larger and that its testes are relatively larger and closer together than in *C. minutum*. Leiper also describes a large genital atrium, but as he says that he made his observations from a single sectioned specimen this cannot be regarded as of specific importance.

The only differences of importance therefore between the two species *C. sellsi* and *C. minutum* are those of size, and as quite as big a range of variation has been found in several series of *C. cotylophorum* examined by the writer, both with regard to the size of the whole worms and of the testes, it is considered probable that *C. minutum* and *C. sellsi* are identical.

Sub-family CLADORCHINAE, Fischöeder, 1901.

Definition.—*Paramphistomidae* : oral sucker with a pair of diverticula.

KEY TO GENERA

- | | | | | | | | |
|--|-----|-----|-----|-----|-----|-----|---------------------|
| 1. Cirrus pouch absent | ... | ... | ... | ... | ... | ... | <i>Pseudodiscus</i> |
| Cirrus pouch present | ... | ... | ... | ... | ... | ... | 2 |
| 2. Testes smooth | ... | ... | ... | ... | ... | ... | <i>Balanorchis</i> |
| Testes lobed or branched | ... | ... | ... | ... | ... | ... | 3 |
| 3. Testes lobed | ... | ... | ... | ... | ... | ... | <i>Pfenderius</i> |
| Testes branched | ... | ... | ... | ... | ... | ... | 4 |
| 4. Testes each consist of four branches like a cross | ... | ... | ... | ... | ... | ... | <i>Chiorchis</i> |
| Testes consist of many long irregular branches | ... | ... | ... | ... | ... | ... | 5 |
| 5. Main portion of uterus posterior to testes, terminal portion runs ventral to testes | ... | ... | ... | ... | ... | ... | <i>Taxorchis</i> |
| Main portion of uterus arches dorsally over testes, terminal portion anterior to testes (as in <i>Paramphistomum</i>) | ... | ... | ... | ... | ... | ... | <i>Cladorchis</i> |

Genus *Watsonius*, Stiles and Goldberger, 1910.

Careful comparison of the definitions of *Watsonius* and *Pseudodiscus*, as given by Stiles and Goldberger, reveal little difference between the two.

In the definition of *Pseudodiscus* they state the genital pore is behind the gut fork; a ductus hermaphroditicus is present; the oral sucker is 'prominently constricted at equator'; the oesophagus has no muscular thickening; and the testes lie side by side near the middle of the worm and are 'cauliflower-like,' which means lobed with lobular subdivisions.

The same points in *Watsonius* are described as follows:—The genital pore is in front of the gut fork; a ductus hermaphroditicus is apparently absent; no mention is made as to whether the oral sucker is constricted or not; the oesophagus has a distal thickening of the muscle layer; and the testes are lobulate lying almost one behind the other. All the other points cited are the same in the two genera, or else are not of any value.

It is repeatedly shown in the present paper that the position of the genital pore in front or behind the gut fork is not even of specific value. As the constriction of the oral sucker is only alluded to in one genus, this point may be discarded. The differential diagnosis thus rests on the apparent absence of a ductus hermaphroditicus, the presence of an oesophageal thickening and the tandem arrangement of the testes in *Watsonius*, against the presence of a ductus hermaphroditicus, the absence of an oesophageal muscular thickening, and the lateral position of the testes in *Pseudodiscus*. In the sub-genus, *Hawkesius* of *Pseudodiscus*, however, Stiles and Goldberger state that there is a pronounced thickening of the posterior part of the oesophagus, and the testes are tandem. In respect of these two characters, the definition of *Pseudodiscus* as given by them cannot be correct. Thus, all the differential points between the genera *Pseudodiscus* and *Watsonius* are eliminated, except the doubtful absence of a ductus hermaphroditicus in the latter. The fact that Stiles and Goldberger in erecting the genus *Watsonius* had only a single specimen cut in transverse section, which they borrowed from Shipley, makes this point of very doubtful value, because it is so difficult to make out a ductus hermaphroditicus in sections of this nature, that it is unsafe to rely on them without confirmation from examination of sagittal sections. Leiper (1913), however, in a short record of *W. watsoni* figures the ductus ejaculatorius and uterus opening separately on the end of a prominent papilla, there being a narrow tongue-like process between the two; thus he apparently confirms

Stiles and Goldberger's statement that a ductus hermaphroditicus is absent. In the same paper, Leiper gives a drawing of *Gastrodiscoides hominis* in which the genital papilla and the two ducts are shown to be practically identical with his figure of *W. watsoni*; the writer has examined sagittal sections of three specimens of *G. hominis* and found a papilla with a long ductus hermaphroditicus in the first specimen (fig. 29), a much shorter ductus hermaphroditicus in the second, and in the third there was no papilla at all and the male and female ducts opened separately at the bottom of a deep atrium (fig. 28). It seems probable that the same variation could be found if a number of *W. watsoni* were examined; this is all the more likely when it is remembered that the same range of variations has been found in every species which the writer has been enabled to examine.

This discussion indicates that there are no clear differences between the genera *Pseudodiscus* and *Watsonius*, and that the latter should be merged in the former.

It should be noted that Railliet, Henry and Joyeux (1912), in recording *Watsonius watsoni* from *Cercopithecus callitrichus*, draw attention to the great similarity between this worm and *Hawkesius*, the sub-genus of *Pseudodiscus* created by Stiles and Goldberger (1910).

Genus *Pseudodiscus*.*

SYNONYMY :—*Watsonius*, Stiles and Goldberger, 1910.

Definition.—*Cladorchinae*: without a cirrus pouch, and testes lobed.

Type species *Pseudodiscus collinsi* (Cobbold, 1875), Sonsino, 1895.

KEY TO SPECIES

Testes side by side	...	...	...	...	...	...	...	<i>P. collinsi</i>
Testes tandem	...	...	...	...	...	...	...	<i>P. hawkesii</i> and <i>P. watsoni</i>

Pseudodiscus collinsi (Cobbold, 1875), Sonsino, 1895.

SYNONYMY :—*Pseudodiscus stanleyi* (Cobbold, 1875), Sonsino, 1895.

First found in the colon of the horse in India.

The material investigated all came from India, and was as follows :—

* Stiles and Goldberger divide the genus *Pseudodiscus* into two sub-genera, viz., *Pseudodiscus*, and *Hawkesius*, but as this serves no useful purpose, it is not used in the present paper.

BOTTLE 1. Four specimens from a pony. These were all about the same size, viz., 7 mm. long and 5 mm. broad, and none contained eggs.

BOTTLE 2. Three specimens from a pony. Two of these were about 7.9 mm. long by 5.4 mm. broad, and both had eggs in their uteri. The third specimen was 5.7 mm. long by 4.4 mm. broad, and had no eggs.

BOTTLE 3. Three specimens from a horse. All three were very small, the largest being only 2.9 mm. long by 1.3 mm. broad.

BOTTLE 4. One specimen from a mule. About medium size.

BOTTLE 5. Three specimens from a horse. They were all small and averaged 4.3 mm. long by 2 mm. broad, and were all obviously immature.

BOTTLE 6. Sixty-four specimens from a horse. The maximum length of any of these worms was 4.8 mm. and the maximum breadth 2.5 mm., the minimum length was 3.2 mm. and the minimum breadth 1.3 mm., with all gradations between these two dimensions. But the longest worm was only 2.1 mm. broad, and the broadest worm was only 4.7 mm. long, therefore, the proportion of length to breadth is not absolute. The average of the whole sixty-four specimens was 4.4 mm. long by 1.9 mm. broad.

BOTTLE 7. Thirty-five specimens from a horse. These worms varied between 8.7 mm. long by 5.7 mm. broad and 5.4 mm. long by 3.2 mm. broad, and several of the larger specimens contained eggs.

(Bottles 6 and 7 were kindly lent by Mr. A. W. N. Pillers, F.R.C.V.S.).

For convenience, the points in which the two worms *P. stanleyi* and *P. collinsi* differ, according to Stiles and Goldberger (1910), are arranged in tabular form (Table VII).

TABLE VII.

	<i>P. collinsi</i>	<i>P. stanleyi</i>
1. Oesophageal portion of sucker.	Relatively broad. A dorsal and ventral 'transverse projecting ridge present.'	Relatively narrow. A dorsal ridge only present.
2. Testes.	Actually and relatively smaller.	Actually and relatively larger.
3. Opening of Laurer's canal.	A little above the posterior border of the acetabulum.	A little behind the anterior border of the acetabulum.
4. Size of acetabulum.	Relatively larger.	Relatively smaller.
5. Position of ovary and shell gland	About level of upper margin of acetabulum.	Distinctly further forward and nearer testes.

It must be noted, however, that Stiles and Goldberger record that they had only a few specimens of each of the two worms and, as they state that no eggs were seen, it is doubtful whether their worms were fully developed.

On looking through the Liverpool material, a doubt was raised in one's mind whether the differences described by Stiles and Goldberger were really of specific value, as it appears from our material that all intermediate stages between the two extremes were to be seen. With a view to examining this more fully, Table VIII was compiled from data obtained from Stiles and Goldberger (1910), from measurements of their drawings, and also from those of nine specimens taken from bottles 1, 2, 3, 6 and 7 of the Liverpool material, as far as possible representing all sizes of the worms.

Comparison of the dimensions given in the table makes it clear that Stiles and Goldberger's differences referring to the relative size of the oesophageal portion of the sucker, and the relative size of testes and acetabulum, are merely due to the stage of development of the various specimens that they examined. In all trematodes the digestive and fixation organs develop earlier than the sexual glands; therefore, it is to be anticipated that the former are relatively larger and the latter relatively smaller in young worms than in older specimens. The differences of position of the ovaries and openings of Laurer's canal are very minute, and the above authors had so little material available, that to give specific value to slight variations in positions of these organs, as they have done, does not appear to be justified.

Historical. Cobbold (1875a) examined thirty-three specimens of this worm from a horse in India, which were sent him by Collins, and he named them *Amphistoma collinsi* because they were smaller than a similar fluke of the elephant (*A. hawkesii*) from the same locality. A few days after publication of this paper he received from Professor Simonds another bottle of flukes from the horse, collected by Stanley in India, and in a paper (Cobbold, 1875b) he named them *Amphistoma stanleyi*, but in doing so, says 'This is apparently nothing more than a large variety of the above?' He made no detailed study of the worms in either case, and no adequate description of the internal anatomy was published until Stiles and Goldberger (1910) examined some of Cobbold's original material. The number of individuals they had for study was not large, therefore they were led to making specific characters of differences which are really due to differences in age of the specimens they examined.

Pseudodiscus stanleyi (Cobb., 1875) is therefore only an immature form of *Pseudodiscus collinsi* (Cobb., 1875) and must be regarded as synonymous with the latter.

TABLE VIII

Worm	Length	Breadth	Ratio of length to breadth	Ratio of diameter of oesophageal part of sucker to diameter of worm	TESTES			ACETABULUM			Distance of ovary and shell gland in front of posterior sucker	Condition of uterus
					Size	Ratio of size to distance between	Ratio of size to size of worm	Total diameter	Diameter of aperture	Ratio of diameter to length of worm		
From Stiles and Goldberger, 1910	<i>P. stanleyi</i> ...	5.5 to 5.6	1 : 1.82	...	...	...	...	1.7	1 to 1.25	1 : 5	...	No eggs.
	<i>P. collinsi</i> ...	3.5 to 4	1 : 1.46	...	...	...	...	1.58 by 1.1	0.5 by 0.7	1 : 3.9	...	No eggs.
	Drawing of <i>P. stanleyi</i> ...	...	1 : 1.54	1 : 12	...	1 : 0.4	1 : 4.8	...	...	1 : 4.5	...	
	Drawing of <i>P. collinsi</i> ...	...	1 : 1.27	1 : 7	...	1 : 2	1 : 7.0	...	...	1 : 4.1	...	
Author's material	Spec. 1 ...	1.4	1 : 2.2	1 : 5.4	0.059	1 : 6.3	1 : 23.6	0.572	0.416	1 : 5	0.05	Rudimentary.
	Spec. 2 ...	2.3	1 : 1.9	1 : 7.3	0.178	1 : 2.9	1 : 13	0.833	0.468	1 : 5.4	0.26	Rudimentary.
	Spec. 3 ...	3.23	1 : 1.6	1 : 10	0.468	1 : 1.3	1 : 7	1.145	0.781	1 : 4.7	0.078	Rudimentary.
	Spec. 4 ...	4.3	1 : 1.3	1 : 11	0.39	1 : 2.6	1 : 11	1.8	0.937	1 : 3.1	Touching	Partly developed.
	Spec. 5 ...	5.2	1 : 1.3	1 : 14.3	0.989	1 : 0.57	1 : 5.2	1.66	1.04	1 : 3.6	0.156	Uterus with eggs.
	Spec. 6 ...	4.16	1 : 1.3	1 : 13	0.572	1 : 1	1 : 7	1.56	0.885	1 : 4.3	0.260	Well developed; no eggs.
	Spec. 7 ...	5.36	1 : 1.26	1 : 14	1.04	1 : 0.5	1 : 7.5	1.822	1.09	1 : 4.4	0.208	Few eggs in posterior part.
	Spec. 8 ...	5.9	1 : 1.3	1 : 17.5	1.04	1 : 0.55	1 : 5.6	1.8	1.09	1 : 4.3	0.31	Well developed; no eggs.
	Spec. 9 ...	5.7	1 : 1.5	1 : 18.3	0.885	1 : 0.64	1 : 6.4	1.875	1.145	1 : 4.7	0.26	Well developed; no eggs.

Pseudodiscus hawkesii (Cobbold, 1875), Sonsino, 1895.

In a list of Trematodes from the Asiatic elephant, Railliet, Henry and Bauche (1914b) give the two following species of Amphistomes :—

(a) *Pseudodiscus hawkesi* (Cobbold, 1875).

SYNONYMY :—

Amphistoma hawkesii, Cobbold, 1875, non Piana and Stazzi, 1900.

Pseudodiscus hawkesi, Sonsino, 1895.

(b) *Watsonius ornatus* (Cobbold, 1882).

SYNONYMY :—

Amphistoma ornatum, Cobbold, 1882.

Pseudodiscus ornatus, Sonsino, 1895.

Amphistoma hawkesi, Piana and Stazzi, 1900.

Hawkesius hawkesi, Stiles and Goldberger, 1910.

Watsonius ornatus, Railliet and Henry, 1912.

Stiles and Goldberger (1910) state that their species *Pseudodiscus* (*Hawkesius*) *hawkesii* is a synonym of *Amphistoma hawkesii*, Cobbold, 1875. It therefore seems clear that *Pseudodiscus hawkesi* (Cobbold, 1875), and *Watsonius ornatus* (Cobbold, 1882) are the same. As Cobbold's original spelling was *hawkesii* and not *hawkesi* the correct name of the worm is *Pseudodiscus hawkesii* (Cobbold, 1875). This worm is easily distinguished from *P. collinsi*, because the testes in *P. hawkesii* are tandem and in *P. collinsi* they are placed side by side.

Pseudodiscus watsoni (Conyngham, 1904).

SYNONYMY :—

Amphistoma watsoni, Conyngham, 1904.

Cladorchis watsoni, Shipley, 1905.

Gastrodiscus watsoni, Verdun, 1907.

Paramphistomum watsoni, Manson, 1908.

Watsonius watsoni, Stiles and Goldberger, 1910.

Watsonius macaci, Kobayashi, 1915.

This species has been found on two occasions, once in man by Watson in 1904, and once in a monkey, *Cercopithecus callitrichus*, by Joyeux in 1912.

Comparison of Stiles and Goldberger's description of *P. hawkesii* and *P. watsoni* show that the two worms are practically identical. The size is somewhat different, however, *P. hawkesii* being 3.5 to 5 mm. in length by 2 mm. to 3 mm. in breadth, and *P. watsoni* 8 mm. to 10 mm. in length by 4 mm. to 5 mm. in breadth; but in *P. hawkesii* no eggs were seen, whereas in the single specimen of *P. watsoni* which these observers examined eggs were present. The difference in size is therefore probably due to difference in age. The writer is of the opinion that the two species are identical, but in view of the facts that he has not been enabled to examine either, and that one worm comes from man and the other from the elephant, he does not feel justified in merging them.

Kobayashi (1915) recorded *Watsonius macaci* from *Macacus cynomolgus* and the same author (1920) gives a description of the worm, adding a footnote to the effect that it is probably identical with the fluke identified as *W. watsoni* by Railliet, Henry and Joyeux (1912). If this is correct, *W. macaci* is a synonym of *P. watsoni*.

Genus *Balanorchis*, Fiscoeder, 1901.

Definition.—*Cladorchinae*: testes not lobed or branched; cirrus sac present and protrusible; genital sucker present.

Type species *Balanorchis anastrophus*, Fiscoeder, 1901.

Host:—*Cervidae* sp. Location:—First stomach. Locality:—Brazil.

Only one species described.

Genus *Pfenderius*, Stiles and Goldberger, 1910.

Definition.—*Cladorchinae*: testes lobed; cirrus sac present; genital sucker absent.

Type species *Pfenderius papillatus* (Cobbold, 1882), Stiles and Goldberger, 1910.

Host:—*Elephas indicus*. Location:—Colon. Locality:—India.

Only one species described.

Genus *Chiorchis*, Fiscoeder, 1901.

Definition.—*Cladorchinae*: with testes each consisting of four branches arranged like a cross; genital sucker absent and cirrus pouch present; vitellaria in two narrow rows along outer side of caeca, each follicle group

has a duct joining direct with the main longitudinal duct ; uterus as in *Paramphistomum*.

Type species *Chiorchis fabaceus* (Diesing, 1838), Fiscoeder, 1901.

Host :—Marine mammals. Location :—small and large intestine.

Locality :—?

Only one species described.

*Taxorchis** (Fiscoeder, 1901), gen. nov.

Definition.—*Cladorchinae* : testes branched ; cirrus pouch present ; genital sucker present ; main portion of uterus posterior to testes, terminal portion runs anteriorly ventral to testes.†

Type species *Taxorchis schistocotyle*, Fiscoeder, 1901.

Host :—*Dictocotyle torquatus*. Location :—Caecum. Locality :—Brazil.

Only one species described.

Genus *Cladorchis*,‡ Fiscoeder, 1901.

Definition.—*Cladorchinae* : with branched testes, genital sucker usually present ; cirrus sac present ; uterus as in the genus *Paramphistomum*.

Type species *Cladorchis pyriformis* (Diesing, 1838), Fiscoeder, 1901.

KEY TO SPECIES

Testes in tandem	...	...	...	...	...	...	...	...	...	1
Testes side by side	...	...	...	...	...	...	...	...	...	2
1. Posterior sucker on ventral surface at										
junction of posterior and middle thirds,										
small and contains no papillae										
...										<i>C. pyriformis</i> (Diesing, 1838),
										Fiscoeder, 1901.
										Host :— <i>Tapirus americanus</i> ,
										S. America

* Fiscoeder classified the species *T. schistocotyle* under the genus *Cladorchis*, sub-genus *Taxorchis*. But the course of the uterus is so different from any other member of the genus that it is considered advisable to place this species in a separate genus.

† The uterus arises from the shell gland just in front of the posterior sucker ; from this point it runs forward near the dorsal surface to the posterior border of the testes, it then turns posteriorly and runs diagonally towards the ventral surface to just in front of the posterior sucker ; after reaching this point it again turns forward and runs close to the ventral surface to the genital pore.

‡ Fiscoeder divided this genus into three sub-genera, viz., *Cladorchis*, *Sticborchis*, and *Taxorchis*. The last has already been dealt with, having been raised to generic rank. *Cladorchis* and *Sticborchis* do not present striking anatomical differences, so they will be considered together, the sub-generic titles being dropped.

- Posterior sucker occupies hinder half of ventral surface ; large (2 mm.-4 mm.) and beset with papillae with special structure *C. asper*, Fiscoeder, 1901.
Host :—*Tapirus americanus*, S. America
2. Pharyngeal pouches projecting from sucker ; genital sucker distinct *C. giganteus* (Diesing, 1838), Fiscoeder, 1901.
Host :—*Dicotyles* spp.
- Pharyngeal pouches so small that they do not show on external wall of sucker ; genital sucker not distinct *C. subtriquetrus* (Rudolphi, 1814), Fiscoeder, 1901.
Host :—*Castor fiber*, *Bos taurus*.

Sub-family *STEPHANOPHARYNGINAE*, Stiles and Goldberger, 1910.

Definition.—*Paramphistomidae* : with a single oral diverticulum.

Only one genus.

Genus *Stephanopharynx*, Fiscoeder, 1901.

Definition.—That of the sub-family.

Type species *Stephanopharynx compactus*, Fiscoeder, 1901.

Only one species recorded.

Stephanopharynx compactus, Fiscoeder, 1901.

Fiscoeder found the worm in *Bos* sp.

The material available to the writer consisted of the following collections :—

1. About 850 specimens.
2. Over one hundred specimens.
3. Ten specimens.

These collections were found in the stomachs of three waterbuck (*Cobus* sp.) at Ngao, N.E. Rhodesia.

Fiscoeder's material consisted of two collections composed of a single specimen in one case and two specimens in the other ; they were found in company with many other *Amphistomata*.

In addition to the single large oral diverticulum, this worm is characterised by the anterior end being hemispherical instead of the usual conical type, and its maximum transverse diameter is about its middle instead of

towards the posterior end which is the ordinary condition in *Paramphistomidae*. The posterior sucker looks ventrally on account of the strong downward curve which the hinder half of the body exhibits, and it is said to have a surprisingly sharp border around its opening. The testes lie one behind the other, the anterior one being about the middle of the body, with the hinder one between it and the posterior sucker. Laurer's canal opens in front of the excretory pore in the mid-line of the dorsal surface, and the genital pore is surrounded by a thickening of the subcuticular muscle not sharply marked off from the parenchyma. The size of these worms is given as 4.8 to 5 mm. in length, 3 mm. in breadth, and 2.5 mm. in thickness. Other anatomical details are of the usual type. The writer found in his collection No. 1 eight worms, and in his collection No. 2 one worm which agreed with Fiscoeder's description in all particulars, except that they were about 7 mm. in length. The remaining numerous specimens, however, at first sight appeared to be very different, as they were sharply pointed at the anterior end and the posterior sucker looked directly backwards, in many cases being widely opened and occupying the whole hinder end of the worm. (Plate VII, fig. B). These worms were of all sizes from tiny specimens about 2 mm. in length up to worms 5.5 mm. in length. Several of these worms were sectioned and it was then found that they agreed with Fiscoeder's species, except that the posterior sucker was relatively larger, and the hinder of the two testes was much nearer the ventral surface than the anterior one (fig. 12). At first it was thought that these points indicated a new species, but it was then noted that none of the worms were gravid, and prolonged search of the ample material failed to reveal any specimen containing eggs. On this account it is considered that they are immature specimens of *S. compactus*, which fact explains the relatively large size of the posterior sucker. The apparently different position of the testes in young worms is not without parallel, for Fiscoeder says that in immature *P. calicophorum*, the anterior testis lies more dorsal than the hinder one, a character which the writer has found disappears when maturity is reached. A further fact in support of the view that the present worms are only immature *S. compactus* is that this species has only been recorded on five occasions (twice by Fiscoeder and three times by the writer) and on two of these it has been found in company with worms of the above closely allied type.

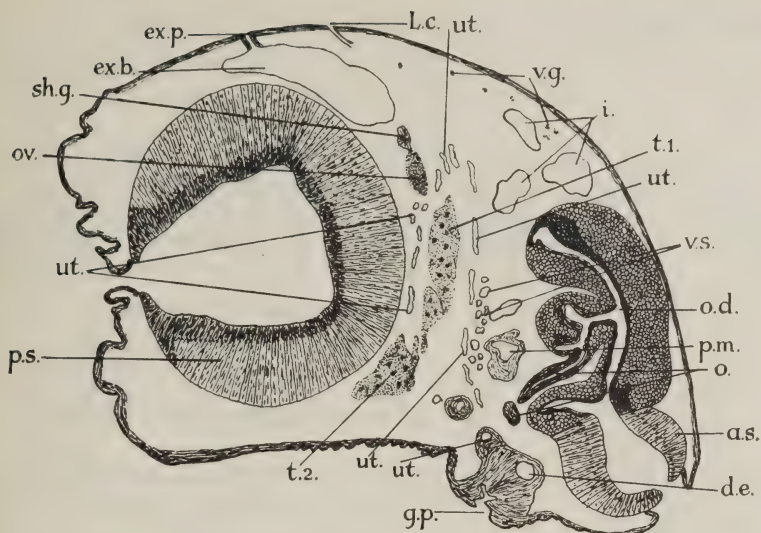


FIG. 12. *Stephanopharynx compactus*. Sagittal section near the mid-line. *a.s.*—anterior sucker; *d.e.*—ductus ejaculatorius; *ex.b.*—excretory bladder; *ex.p.*—excretory pore; *g.p.*—genital pore; *i.*—intestine; *L.c.*—Laurer's canal; *o.*—oesophagus; *o.d.*—oral diverticulum; *ov.*—ovary; *p.m.*—pars muscosa; *p.s.*—posterior sucker; *sh.g.*—shell gland; *n.*—dorsal testis; *t.2.*—ventral testis; *ut.*—uterus; *v.g.*—vitelline gland; *v.s.*—vesicula seminalis. $\times 14$.

Family GASTROTHYLACIDAE, Stiles and Goldberger, 1910.

Definition.—*Amphistomata*: with a ventral pouch.

KEY TO GENERA

- | | | | | | | |
|--|-----|-----|-----|-----|-----|-----------------------|
| 1. Uterus crosses from one side of body to the other near the middle of the worm | ... | ... | ... | ... | ... | <i>Gastrothylax</i> |
| Uterus lies in centre of body for its whole length | ... | ... | ... | ... | ... | 2 |
| 2. Testes side by side | ... | ... | ... | ... | ... | <i>Carmyerius</i> |
| One testis dorsal of the other, both in mid-line | ... | ... | ... | ... | ... | <i>Fischboederius</i> |

Genus *Gastrothylax*, Poirier, 1883.

Fischboeder (1903) placed all the known *Paramphistomidae* with a ventral pouch in the genus *Gastrothylax*. He divided the species in this genus into five groups, using the shape of the ventral pouch on cross-section as the distinguishing feature. His list is as follows:—

Genus *Gastrothylax*.

(a) Transverse section of pouch triangular with apex dorsally directed and apical angle undivided.

1. *G. crumenifer* (Crepl.).
2. *G. compressus*, Brandes.

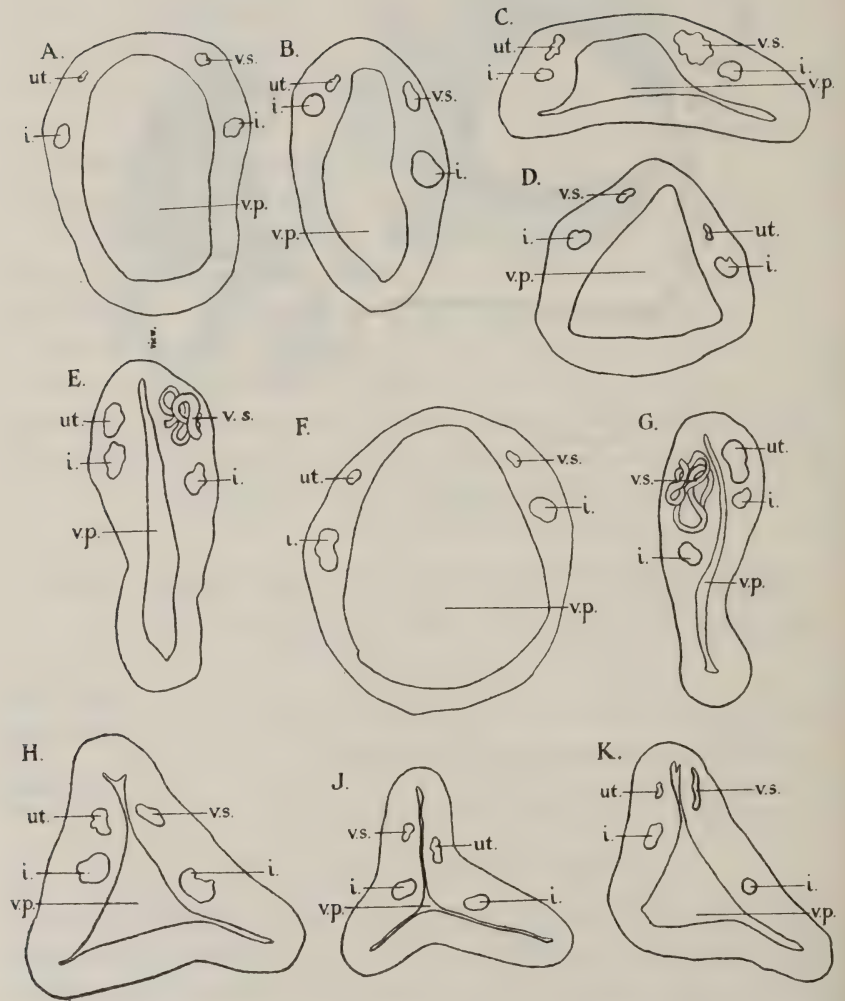


FIG. 13. *Gastrotbylax crumenifer*. Transverse sections through the middle of ten specimens showing variation in shape of ventral pouch. *i.*—intestine; *ut.*—uterus; *v.p.*—ventral pouch; *v.s.*—vesicula seminalis. $\times 9$.

(b) Transverse section of pouch triangular with apex dorsally directed and apical angle bifurcated.

3. *G. gregarius*, Looss.

(c) Transverse section of pouch circular.

4. *G. spatiosus*, Brandes.

(d) Transverse section of pouch triangular with apex ventrally directed.

5. *G. synethes*, Fischdr.

6. *G. elongatus*, Poirier.

7. *G. cobboldi*, Poirier.

8. *G. mancupatus*, Fischdr.

(e) Transverse section of pouch triangular with apex ventrally directed. The two basal angles bifurcated.

9. *G. minutus*, Fischdr.

The writer has carefully investigated the shape of the ventral pouch in cross section in all the species he has had at his disposal. Fig. 13 illustrates transverse sections at the mid point of ten specimens of *G. crumenifer*. All the specimens agreed in other anatomical details and all came from the same bottle. Fig. 14 represents similar sections of six specimens of *G. spatiosus*.

On examining the drawings it will be seen that fig. 13, D, corresponds with Fiscoeder's group (a), fig. 13, H and K, correspond with his group (b), and fig. 13, F, is so nearly circular as to correspond with his group (e). Fig. 13, A, B, C, E and J, do not agree with any of Fiscoeder's five groups. Therefore, in a series of ten specimens of a single species three of Fiscoeder's five groups are represented, and the others cannot be classified by this method. If fig. 13, D, H and K, are further examined, it will be noted that they are all triangular with the apex dorsal, whereas in fig. 14, B and D, which approach the triangular shape, the apex is ventral. This at first seems to indicate that a division between the species might be made on the fact that when the pouch is triangular, the apex is ventral in some species and dorsal in others. But fig. 14, A, upsets this view, because here is a worm considerably distorted in fixation with the dorsal surface drawn to the right and the ventral surface displaced to the left. The ventral pouch in this case is a narrow triangle with the base to the right. If this worm could be straightened up, one would have a specimen with the base

of the ventral pouch looking towards the ventral surface, unlike the other examples of the same species in which the base of the pouch, when triangular, is dorsally directed. From this it will be seen that the cross section of the ventral pouch may assume almost any shape and cannot therefore be regarded as of any use in diagnosis.

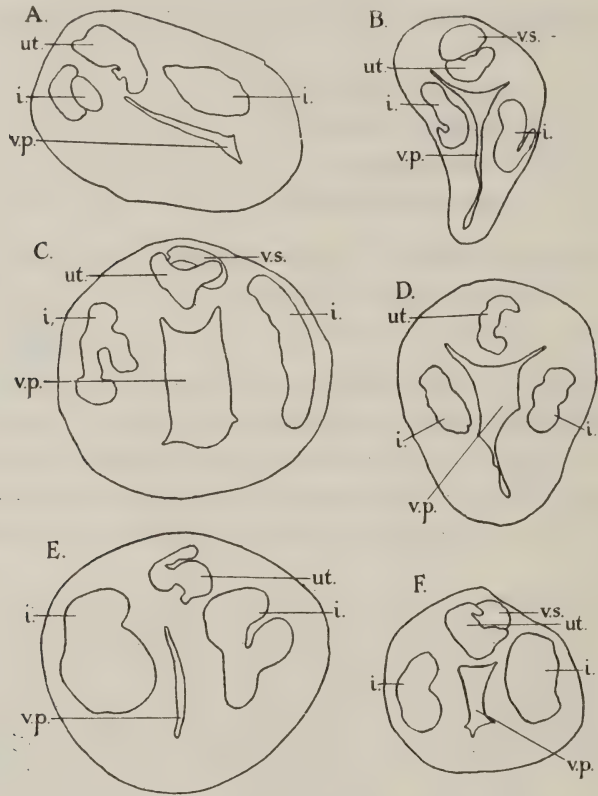


FIG. 14. *Carmynerius spatiosus*. Transverse sections through the middle of six specimens showing variations in shape of ventral pouch. i.—intestine; ut.—uterus; v.p.—ventral pouch; v.s.—vesicula seminalis. $\times 9$.

The shape of the ventral pouch when seen from the side also varies considerably, as reference to figs. 15, 16, and 17 will readily show. For the most part the changes in shape of the pouch when viewed in this position are caused by outpocketings from the posterior end along the dorsal and ventral surfaces of the testes, but in a few cases a narrow prolongation may also occur from the dorso-anterior part of the pouch (see fig. 17, C). In addition to differing as a whole, the pouch also exhibits varying form in

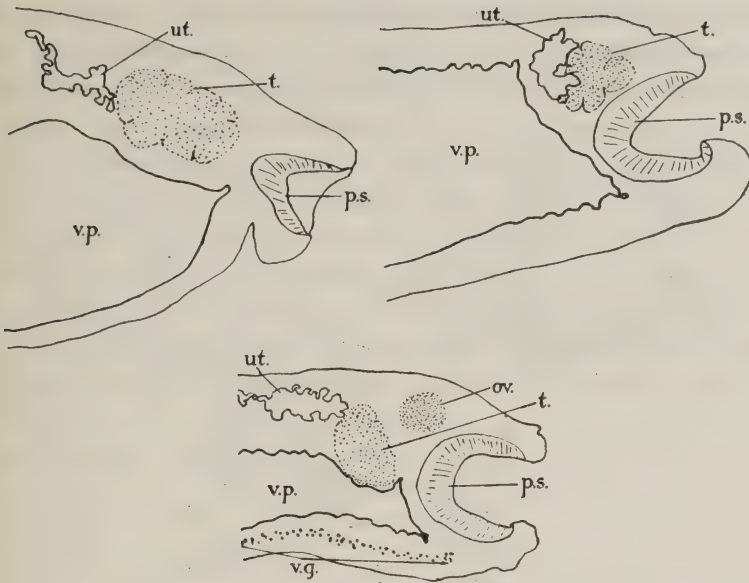


FIG. 15. *Gastrothylax crumenifer*. Sagittal sections near the mid-line of three specimens to show the shape of the posterior end of the ventral pouch. *ov.*—ovary; *p.s.*—posterior sucker; *t.*—testis; *ut.*—uterus; *v.g.*—vitelline gland; *v.p.*—ventral pouch. $\times 9$.

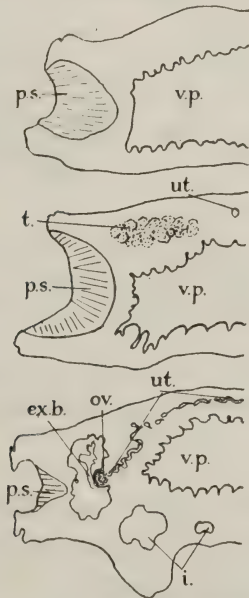


FIG. 16. *Gastrothylax crumenifer*. Three sagittal sections from a single specimen at different levels, showing change in shape of posterior end of pouch in one worm. *ex.b.*—excretory bladder; *i.*—intestine; *ov.*—ovary; *p.s.*—posterior sucker; *ut.*—uterus; *v.p.*—ventral pouch. $\times 9$.

different sections of the same worm (fig. 16). It will be noted later that Stiles and Goldberger use the presence of a ventral prolongation of the pouch beneath the testes as a specific character in at least one instance.

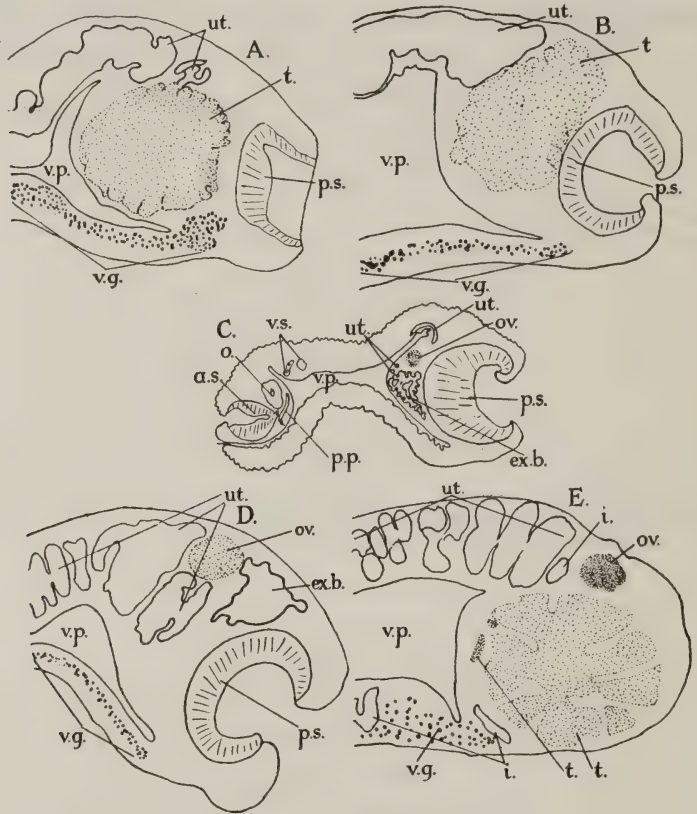


FIG. 17. *Carmyerius spatiosus*. . Sagittal sections of five specimens near the mid-line showing variation in shape of posterior end of pouch. A, B, D, and E—Gravid worms. C—Immature worm. a.s.—anterior sucker; ex.b.—excretory bladder; i.—intestine; o.—oesophagus; ov.—ovary; p.p.—pars prostatica; p.s.—posterior sucker; t.—testis; ut.—uterus; v.g.—vitelline gland; v.p.—ventral pouch; v.s.—vesicula seminalis. $\times 9$.

The above demonstration of the presence or absence of this prolongation in a single species (fig. 17) is held to prove that this character is of no value for specific diagnosis.

Genus *Gastrothylax* (Poirier, 1883), s. str., Stiles and Goldberger, 1910.

Definition.—*Gastrothylacidae*: with the uterus crossing from one side of the body to the other about its middle.

Type species *Gastrothylax crumenifer* (Creplin, 1847).

Only one species recorded.

Gastrothylax crumenifer (Creplin, 1847).

SYNONYMY :—*Gastrothylax compressus*, Brandes, 1898.

Stiles and Goldberger (1910) revised Fiscoeder's classification and restricted the genus *Gastrothylax* to include only those species in which the uterus crosses from one side of the worm to the other about midway between the anterior and posterior extremities. The result of this restriction is that the genus now contains only two species, viz., *G. crumenifer* and *G. compressus*. The writer has not been able to consult the original descriptions of these species, but Fiscoeder (1903) describes them very fully and use has been made of this work in the present discussion.

The points of difference between these two worms are summarised from Fiscoeder (1903) in Table IX.

TABLE IX.

Points of difference between *G. compressus* and *G. crumenifer*.

	<i>G. compressus</i>	<i>G. crumenifer</i>
Length of oesophagus ...	400 μ to 500 μ	1.2 mm. to 1.5 mm.
Gut caeca	Almost straight. End 300 μ to 500 μ anterior to testes.	Wavy. End behind anterior border of testes.
Uterus	Not so convoluted.	More convoluted.
Eggs	Not so numerous. 115 μ to 125 μ by 60 μ to 65 μ .	More numerous. 125 μ to 135 μ by 65 μ to 70 μ .

In the present instance the material available for examination consisted of two bottles containing several hundred specimens. One collection came from a bullock in India and the other from a bullock in Hong Kong. Examination of a large number of these worms has shown that like all other *Amphistomata*, they are liable to considerable variation. In our collections there are many worms which could be identified as one or other of the above species, and there are just as many which would fit either species just as well. It is therefore considered that these two species have been separated from one another on points of individual variation, and that the differences are so variable in degree that in all probability *G. compressus* is merely a synonym of *G. crumenifer*.

Genus *Fischoederius*, Stiles and Goldberger, 1910.

Definition.—*Gastrothylacidae* : with the uterus in the centre of the body for its whole length ; one testis dorsal of the other.

Type species *Fischoederius elongatus* (Poirier, 1883), Stiles and Goldberger, 1910.

KEY TO SPECIES

Gut caeca extend at least to testes	<i>F. cobboldi</i>
Gut caeca never extend further than just beyond middle of body	<i>F. elongatus</i>

Fischoederius elongatus (Poirier, 1883), Stiles and Goldberger, 1910.

SYNONYMY :—

Fischoederius fischoederi, Stiles and Goldberger, 1910.

Fischoederius siamensis, Stiles and Goldberger, 1910.

Fischoederius ceylonensis, Stiles and Goldberger, 1910.

First found in the stomach of *Palonia frontalis* in Java.

The material available to the writer consisted of about 25 specimens obtained from a bullock in Hong Kong.

Eight specimens were cleared in carbolic acid and their examination showed that the worm closely agrees with Fischoeder's (1903) description, with the proviso that this author does not take cognisance of individual variations. For instance, Fischoeder states that the caeca end within the beginning of the hinder half of the body, but in the eight specimens examined, this was found to be the case only in three of them ; in one the caeca ended exactly at the junction of the anterior and posterior halves of the body, and in the remaining four specimens they ended at varying distances up to as much as 1 mm. in front of it. In three cases the two caeca were of unequal length ; in the most marked instance the gut on one side was 1 mm. longer than on the other. In some of the worms examined, the caeca were as convoluted as Fischoeder shows in his fig. 59, but in others they were nearly straight, and furthermore some caeca presented short dilated portions in various parts of their course, while in others they were of uniform diameter throughout.

Fischoeder also says that the testes lie one above the other near the mid-line, the ventral one being slightly to the right of the mid-line and slightly posterior to the dorsal, which is rather to the left of the mid-line. This was true of some of the specimens examined, but in others one testis appeared to lie directly above the other, and both of them were exactly in the mid-line.

Fischoederius fischoederi, Stiles and Goldberger, 1910.

This species is stated to have been made from a single specimen found in a bottle containing a number of worms which had been determined by Fischoeder as *G. elongatus* (*F. elongatus*). They distinguished it from the latter on the ground that the gut caeca were very slightly longer, and that the ovary and shell gland lie between the testes in *F. fischoederi*, which they state is not the case in *F. elongatus*. With regard to the position of the ovary in *F. elongatus*, Fischoeder (1903) states:

‘Der fast kuglige Keimstock (0.3 bis 0.35 mm. im Durchmesser) liegt dorsal von der Schalendrüse, etwas seitlich von der Medianlinie dicht hinter und etwas median von dem meist nach hinten herabhängenden dorsalen Ende des vordern Hodens (Text fig. L).’

It will be noted that he makes no reference to the other testis, but Text fig. L, to which he refers, shows the ovary and shell gland lying between the two testes, but a little further back than Stiles and Goldberger show them in fig. 2. As it is recognised that the ovary varies slightly in position in most species, this difference cannot be considered of specific importance, especially as it relates to an isolated specimen taken from a collection of *F. elongatus* which had already been determined by Fischoeder. It is therefore considered that *F. fischoederi* is a synonym of *F. elongatus*.

Fischoederius siamensis and *F. ceylonensis*, the other two new species made by Stiles and Goldberger, are separated from *F. elongatus* because they do not exhibit the prominent bulging round the genital pore which these authors state is present in *F. elongatus*. It is true Fischoeder (1903) in his description of *F. elongatus* mentions this bulging, but from the experience of the writer, it is concluded that the bulging is a variable character and is similar to that which may be found in any species of the group *Amphistomata* and is accordingly of no specific value. It is therefore considered that *F. siamensis* is synonymous with *F. elongatus*.

F. ceylonensis was established as a new species on a single specimen taken from a bottle of *G. synethes*. Stiles and Goldberger distinguish between *F. ceylonensis* and *F. siamensis* by two points; firstly, the testes in *F. ceylonensis* are directly one above the other and in *F. siamensis* they are slightly diagonal; and secondly, the ventral pouch in *F. ceylonensis* extends ventral to the testes, whereas in *F. siamensis* this extension of the ventral pouch does not occur. The individual variations which may be found in the ventral pouch have, however, already been fully discussed,

and it is considered that the differences between *F. ceylonensis* and *F. siamensis* are not of specific value, more especially as the diagnosis of one of them rests on a single specimen.

Fischoederius cobboldi (Poirier, 1883), Stiles and Goldberger, 1910.

First found in the stomach of *Palonia frontalis* in Java.

No material of this species was available to the writer.

From Fischoeder's description, the distinguishing feature between *F. cobboldi* and *F. elongatus* is the difference in position of the termination of the caeca. In *F. cobboldi* they end opposite the base of the sucker, that is posterior to the testes and near the hinder end of the worm, and in *F. elongatus* they end about the middle of the worm. Although it has been shown that the point of termination of the caeca is subject to variations in practically all species of the group, in the present instance the differences between the two species under discussion are so marked that it is unlikely that they can be explained in this manner. It is accordingly considered that *F. cobboldi* and *F. elongatus* can be distinguished by the difference in length of the caeca.

Genus *Carmyerius*, Stiles and Goldberger, 1910.

SYNONYMY :—*Wellmanius*, Stiles and Goldberger, 1910.

Definition.—*Gastrothylacidae* : with the uterus in the centre of the worm for its whole length ; testes side by side.

Type species *Carmyerius gregarius* (Looss, 1896), Stiles and Goldberger, 1910.

KEY TO SPECIES

- | | | | | | |
|----|--|-----|-----|-----|-----------------------|
| 1. | Genital pore lies outside ventral pouch | ... | ... | ... | <i>C. exoporus</i> |
| | Genital pore lies within ventral pouch | ... | ... | ... | 2 |
| 2. | Excretory canal and Laurer's canal unite before reaching the surface | ... | ... | ... | <i>C. wenyoni</i> |
| | Excretory canal and Laurer's canal do not unite | ... | ... | ... | 3 |
| 3. | Cross section of ventral pouch shows five angles | ... | ... | ... | <i>C. cruciformis</i> |
| | Cross section of ventral pouch does not show five angles | ... | ... | ... | 4 |
| 4. | Gut caeca extend to testes | ... | ... | ... | <i>C. spatiosus</i> |
| | Gut caeca do not extend beyond middle of worm | ... | ... | ... | <i>C. gregarius</i> |

Stiles and Goldberger made this genus to include all the species of Poirier's *Gastrothylax* in which the uterus occupies a central position for its whole length, the testes lie side by side, and the vas deferens is without a straight portion at its commencement. This included the following five

species: *C. synethes* (Fischoeder, 1901), *C. gregarius* (Looss, 1896), *C. spatiosus* (Brandes, 1898), *C. mancupatus* (Fischoeder, 1901), and *C. minutus* (Fischoeder, 1901). They divide the above five species into two groups, because the first two worms are said to have a genital atrium with a large ventral chamber and the last three a genital atrium without a ventral chamber. These characters have been fully discussed already and it has been shown that presence or absence of chambers in the atrium, or even the existence of the atrium itself, are purely matters of chance, so that it seems reasonable to assume that this point is of no value in the present instance. Differences in shape of the ventral pouch are also mentioned in the definitions of the various species. The unreliability of this character has already been dealt with.

Carmyerius spatiosus (Brandes, 1898).

SYNONYMY:—

Carmyerius synethes, Fischoeder, 1901.

Carmyerius minutus, Fischoeder, 1901.

Carmyerius mancupatus, Fischoeder, 1901.

Gastrothylax bubalis, Innes, 1912.

Wellmanius wellmani, Stiles and Goldberger, 1910.

First found in the stomach of *Bos taurus* in Arabia.

Material available:—Two collections from Ngoa, N.E. Rhodesia; the host in one case was a roan (*Hippotragus equinus*) and in the other a reedbuck (*Cervicapra* sp.).

As the four species *C. spatiosus*, *C. synethes*, *C. minutus* and *C. mancupatus* only differ in minute points apart from those already dealt with, they will be discussed together.

According to Stiles and Goldberger's key, the only point by which these four species may be distinguished are minute differences in the gut caeca. They write that in *C. synethes* the caeca are 'corkscrew-like, rather narrow and long'; in *C. spatiosus* they are 'straight, narrow and rather long'; in *C. mancupatus* they are 'rather sinuous, narrow, and long'; and in *C. minutum* they are 'swollen in their caudal half and are rather long.' In all four cases the caeca are said to end in the 'fourth zone.' Twenty specimens were cleared in carbolic acid and it was found that the degree of convolution of the caeca was so variable as to be of no use for diagnosis. With regard to differences in diameter of various parts of the caeca, they were found swollen or contracted in any part of their course or of uniform

diameter throughout. Fig. 18, A and B are drawings of the two caeca in a single worm showing alternate contractions and dilatations; fig. 18, C, is a drawing from another specimen showing the gut of uniform diameter from end to end. It is therefore clear that dilatation of a special part of the caeca is of no diagnostic value.

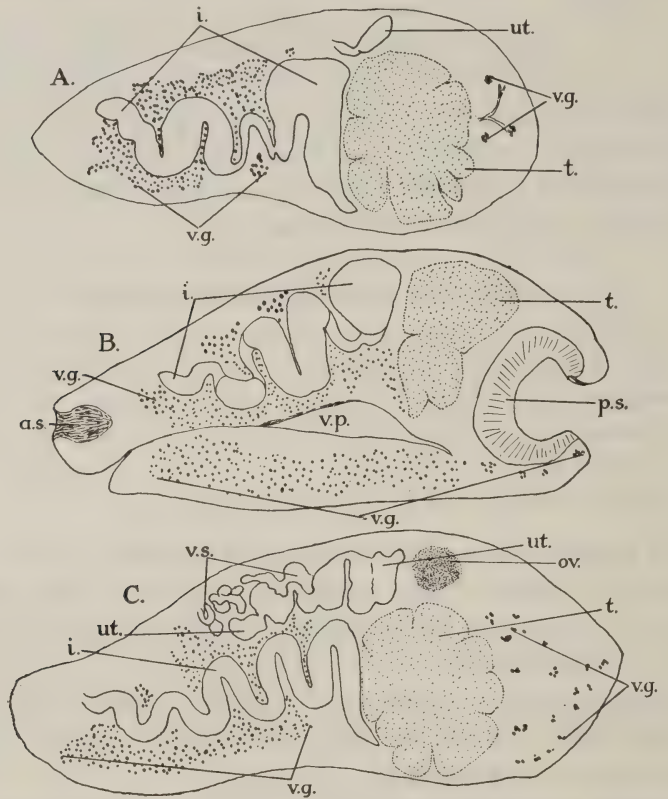


FIG. 18. *Carmyerius spatiosus*. Sagittal section to show variation in calibre of gut. A and B—Showing the two sides of the same worm. C—Section of another worm. a.s.—anterior sucker; i.—intestine; ov.—ovary; p.s.—posterior sucker; t.—testes; ut.—uterus; v.g.—vitelline gland; v.p.—ventral pouch; v.s.—vesicula seminalis. $\times 9$.

Fischoeder (1903) mentions one or two other small points of difference, viz., the genital pore lies further posteriorly in *C. synethes* than in any other species, being about 1 mm. behind the entrance to the ventral pouch; but as he gives 0.8 mm.-0.9 mm. and 0.7 mm.-0.8 mm. for the same dimension in *C. spatiosus* and *C. manicupatus* respectively, it cannot be considered justifiable to regard this of specific value, especially as he gives the limits of variation in length of the worms as being between 6 mm.-12 mm. for the three species.

Fischoeder states that *C. minutus* is 4 mm.-5 mm. in length ; then he remarks that some specimens are longer and thinner than this, but gives no other measurements. This point cannot be regarded of any value when he says that *C. spatiosus*, *C. synethes* and *C. mancupatus* are 9 mm.-12 mm., 7 mm.-11 mm., and 6 mm.-11 mm. in length respectively. Another point of difference claimed between *C. minutus* and the other three species, is that the ovary and shell gland are said to be more strongly developed in the former. But difference in size of the genital organs is so dependent on the age of an individual that it cannot be regarded as a satisfactory diagnostic character.

From the above observations it is concluded that Fischoeder's three species, *C. synethes*, *C. mancupatus* and *C. minutus* are synonyms of *C. spatiosus* (Brandes).

Carmyrius wenyoni (Leiper, 1908).

Found in the stomach of *Cobus maria* at Taufikia, White Nile.

It is not included in Stiles and Goldberger's (1910) classification. It is similar in most respects to *C. spatiosus*, but there is one point by which it may be clearly distinguished, and that is that the excretory canal and Laurer's canal unite before reaching the surface of the worm and open by a common pore. This character is very remarkable as it has not been observed in any other species.

Carmyrius cruciformis (Leiper, 1910).

The material available for study consisted of a single collection of over one hundred specimens from a hippopotamus killed in Lake Victoria, Nyanza.

This worm was first described by Leiper who states that he only had immature material. Leiper gives the length of this worm as from 0.5 mm. to 0.8 mm.; this is apparently a mistake for 5 mm. to 8 mm. because he gives the dorso-ventral diameter of the posterior sucker as 0.9 mm. with a muscle wall of 1.8 mm. in thickness. Some of the writer's specimens contained eggs in the uterus and these worms measured 5 mm. to 7 mm. in length with a maximum diameter of about 1.5 mm.; they agree in general anatomical details with Leiper's description. The uterus

was observed to pursue a slightly wavy course along the centre of the dorsal surface; the most heavily gravid specimen only contained about thirty eggs disposed in a single chain and not closely packed into the uterus in the usual manner. Eggs removed from one specimen measured about $135-140\mu$ in length by $80-84\mu$ in breadth; on account of the small size of the worm they appeared relatively large. Leiper named this worm 'cruciformis' because he says the ventral pouch always shows five angles in cross section no matter how contracted the worm may be, and this frequently appears as a cross. The writer cut eight specimens transversely, and although the pouch of three of them exhibited five angles none were at all like a cross and the other five specimens exhibited just as extensive variation as do all *Gastrothylacidae* in respect of the shape of the pouch.

This worm is essentially the same as *C. spatiosus* in details of anatomy, but is easily distinguished from this species by its minute size even in the gravid state.

Gastrothylax bubalis, Innes, 1912.

This worm was recorded by Innes (1912) as a new species. It was found in the stomach of the Hartebeest in Rhodesia.

The general anatomy of the worm is apparently in no way different from *C. spatiosus*; to quote from Innes the identification of the species is based on the following characters:—

'The excretory vesicle of this species is unique both in position and outline. It is situated immediately in front of the posterior sucker and behind the shell gland, while in other species it has a more or less lateral position. The great irregularity of its outline is striking.'

No authority is given for the statement that the excretory bladder lies in a more or less lateral position in other species, and Fiscoeder (1903) states that in *G. spatiosus*:

'Die sehr grosse Excretionsblase liegt zwischen der Bauchtasche und dem Saugnapfe einerseits und den beiden Hoden andererseits (fig. 52c. u. 54).'

And in all other species of the genus that he deals with he describes it in a similar position, only alluding to slight alterations due to change of shape, and his figures all show it in the same position as it is seen, Innes' fig. 7. It therefore seems clear that this difference claimed by Innes does not exist. With regard to his other point, viz., the irregularity of the excretory bladder, it may be observed that irregularity of outline is

characteristic of a partly distended bladder in any species, and is obviously of no specific value. From this it is concluded that the species *G. bubalis* is only a synonym of *C. spatiosus*.

Carmyerius gregarius (Looss, 1896), Stiles and Goldberger, 1910.

First found in the stomach of *Bos bubalis* in Egypt.

Material available.—A single collection of about 25 specimens from a buffalo.

This species is easily distinguished from the other species of the genus, as the gut caeca are very short. Of ten specimens cleared in carbolic acid only one was found in which the caeca reached the middle of the worm; in all the others they ended at varying distances anterior to this point. For the most part the caeca were of uniform diameter throughout, but in one specimen they exhibited a swelling about their middle and in another there was a club-shaped swelling at their extremities. Although variation in the length of the caeca has been found unreliable for specific diagnosis when the range is slight, they are, however, so much shorter in *C. gregarius* than in *C. spatiosus* that this difference is considered of specific value in the present instance.

Carmyerius exoporus, n.sp.

Found in the stomach of a *Tragelaphus spekei* in Nyasaland.

The material available was a single collection of over three hundred specimens.

EXTERNAL ANATOMY

All stages of growth were represented in the collection, from worms no bigger than a raspberry seed up to gravid worms measuring over 11 mm. in length. But even in gravid worms the shape and size was subject to great variation (see Plate VII, A). It will be noted in this plate that in some cases the worms are fully extended (9) and in others they are in a state of contraction (7). In view of the great variation in shape that exists, it is not considered worth while giving a detailed description, but as a rough indication of what the size of gravid worms is, it may be stated that they varied from 11.5 mm. in length by 2.6 mm. in breadth to 5 mm. in length by 3.8 mm. in breadth. In all cases the worms were practically circular on cross section. As the worms are not curved ventrally, the opening of the anterior sucker lies at the extreme anterior end and looks directly

forwards. The opening of the ventral pouch lies in the mid-line of the ventral surface close behind and below the oral opening, and between the two is the opening of the genital pore, which is thus outside the ventral pouch. This character is sufficient to distinguish the present species from any other member of the genus *Carmyrius*, as in all the hitherto described species the genital pore opens within the ventral pouch. The posterior sucker, as a rule, looks directly backwards, but in a few cases it is slightly tilted ventrally.

INTERNAL ANATOMY

The general arrangement of the organs of this species is very similar to *G. spatiosus* and on that account only the briefest description is necessary.

Muscular system. This system exhibits no special characters.

Nervous system. This system was not investigated.

Anterior sucker. The anterior sucker is of the typical globular shape, oval in section.

Intestines. The oesophagus arises from the posterior end of the anterior sucker and after pursuing a dorsally curving course of about 300μ , it divides into the two gut caeca. These two canals pursue a wavy course along each side of the worm and terminate about the level of the testes.

Posterior sucker. The posterior sucker is fairly thick-walled and looks directly backwards or slightly towards the ventral surface (figs. 20, 21 A, and 25).

Excretory system. The excretory bladder is of the usual type and its degree of convolution varies with its state of distension. The excretory canal runs dorso-posteriorly and opens in the mid-line of the dorsal surface above the anterior border of the posterior sucker (fig. 20).

Genitalia. Testes. The testes are large lobed organs lying one on each side of the mid-line near the hinder end of the worm (fig. 21 A).

Vas deferens. This duct is composed of the usual three portions, the vesicula seminalis, the pars muscosa, and the pars prostatica. The first two portions are much convoluted and occupy the anterior third of the centre of the dorsal part of the worm. The pars prostatica is relatively long and straight, and runs directly forwards to enter the genital papilla (figs. 19 and 21, B).

Genital pore. The genital pore is surrounded by a muscular thickening not marked off from the parenchyma and it opens in the middle of the worm between the oral opening dorsally and the opening of the ventral pouch

ventrally (figs. 19 and 22). It is of the usual type in structure and the appearance shown in the figures is not the only one met with, as the genital papilla is capable of complete retraction or extrusion as in other species. In the figures it is in the intermediate condition.

Ovary and shell gland. These two structures lie between the testes on one hand, the base of the ventral pouch in front and the posterior sucker on the other (figs. 20 and 21 A).

Laurer's canal. Laurer's canal runs almost directly dorsally from the shell gland and opens in the mid-line well in front of the excretory pore (fig. 20).

Vitellaria. For the most part these glands lie in the ventral portion of the worm, but they extend for varying distances on each side towards the dorsal surface. As a rule, they extend from the posterior end of the anterior sucker in front, to opposite the testes behind, but in a few cases follicles were found close to the posterior end of the worm, and surrounding the opening of the posterior sucker (figs. 19, 20, 21, A, and 25).

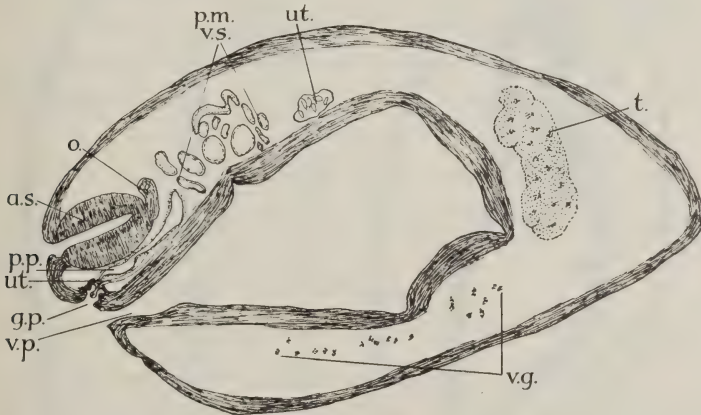


FIG. 19. *Carmyerius exoporus*, n.sp. Sagittal section. a.s.—anterior sucker; g.p.—genital pore; o.—oesophagus; p.m.—pars muscosa; p.p.—pars prostatica; t.—testis; ut.—uterus; v.g.—vitelline gland; v.p.—ventral pouch. $\times 18$.

Uterus. The uterus pursues a wavy course along the centre of the dorsal surface; anteriorly it terminates by running ventral to the pars prostatica and uniting in the genital papilla with the male duct (figs. 21 B and 22).

Eggs. These are oval, operculated and measure about 115μ to 130μ in length by 60μ to 68μ in breadth, but they were only taken from one specimen, so these dimensions must be regarded as only approximate.

Ventral pouch. The ventral pouch is somewhat characteristic in

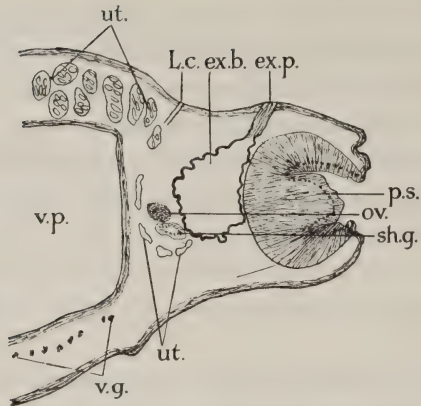


FIG. 20. *Carmyerius exoporus*, n.sp. Sagittal section of posterior end of worm. *ex.b.*—excretory bladder; *ex.p.*—excretory pore; *L.c.*—Laurer's canal; *ov.*—ovary; *p.s.*—posterior sucker; *sh.g.*—shell gland; *ut.*—uterus; *v.g.*—vitelline gland; *v.p.*—ventral pouch. $\times 16$.

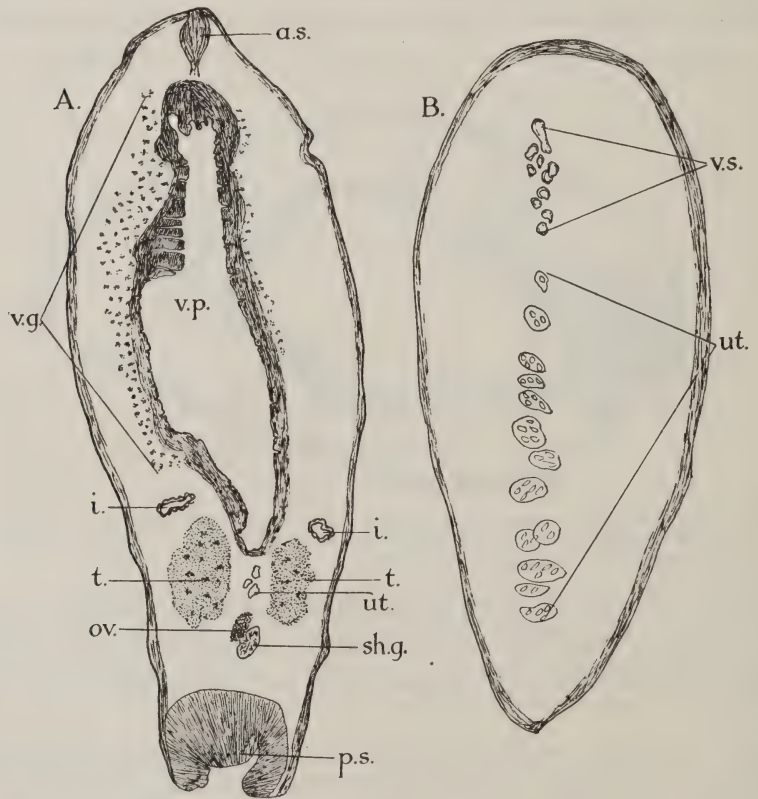


FIG. 21. *Carmyerius exoporus*. Coronal sections. *A*—About middle of worm. *B*—Near dorsal surface. *a.s.*—anterior sucker; *i.*—intestine; *ov.*—ovary; *p.s.*—posterior sucker; *sh.g.*—shell gland; *t.*—testes; *ut.*—uterus; *v.g.*—vitelline gland; *v.p.*—ventral pouch; *v.s.*—vesicula seminalis. $\times 8$.

some cases, in that on cross section about its middle it often shows six points or angles ; but it is subject to so many variations that this cannot be regarded as a diagnostic character. These variations are well shown in figs. 23, 24 and 25.

DIAGNOSIS

As this worm is easily distinguished by the fact that the genital pore opens outside the ventral pouch, the name *Carmyerius exoporus*, n.sp., is suggested.

Genus *Wellmanius*, Stiles and Goldberger, 1910.

This genus was established by Stiles and Goldberger to include a new species *Wellmanius wellmani* which was obtained from the stomach of a reed bok (*Cervicapra bohor*) at Benguella, West Africa. The sole distinguishing character between *Wellmanius* and *Carmyerius* is that in the former the first part of the vesicula seminalis is straight, and in the latter it is coiled from the commencement. This seems a very small point on which to establish a genus, especially when it is found that the beginning of the vesicula seminalis cannot be made out with accuracy in most gravid specimens whatever the species may be, because it is overlaid by the uterus. *W. wellmani* appears to the writer to be synonymous with *C. spatiosus*.

Family *GASTRODISCIDAE*, Stiles and Goldberger, 1910.

Definition.—*Amphistomata* : body usually flattened and divided into anterior and posterior portions.

KEY TO GENERA

1. Anterior portion large and flat, and posterior portion smaller and spherical
Homalogaster
- Anterior portion small and conical, posterior portion large and flat ... 2
2. Genital pore on anterior portion, ventral surface of posterior portion not covered with papillae ... *Gastrodiscoides*
- Genital pore on posterior portion, ventral surface of posterior portion covered with papillae ... *Gastrodiscus*

Genus *Gastrodiscus*, Leuckart, 1877.

Definition.—*Gastrodiscidae* : anterior portion small and conical, posterior portion large and flat ; genital pore on posterior portion, ventral surface of posterior portion covered with papillae.

Type species *Gastrodiscus aegyptiacus* (Cobbold, 1877), Looss, 1896.

KEY TO SPECIES

- Genital pore less than 1 mm. from anterior border of posterior portion *G. aegyptiacus*
 Genital pore over 1 mm. from anterior border of posterior portion *G. secundus*

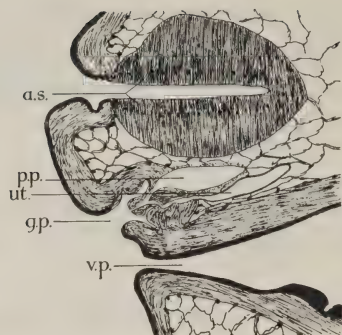


FIG. 22. *Carmyerius exoporus*, n.sp. Sagittal section on enlarged scale to show genital pore. a.s.—anterior sucker; g.p.—genital pore; p.p.—pars prostatica; ut.—uterus; v.p.—ventral pouch. $\times 30$.

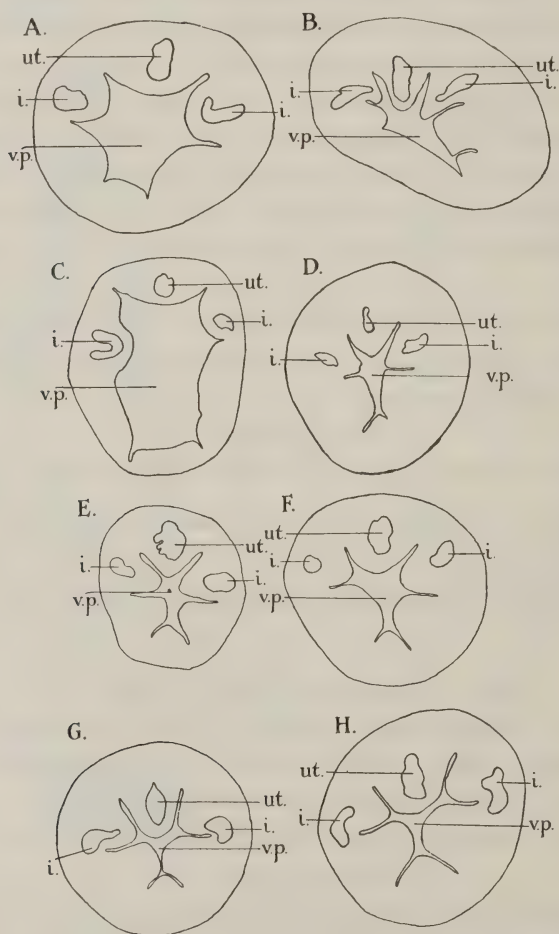


FIG. 23. *Carmyerius exoporus*, n.sp. Transverse section of eight specimens near the middle showing variation in shape of ventral pouch. i.—intestine; ut.—uterus; v.p.—ventral pouch. $\times 9$.

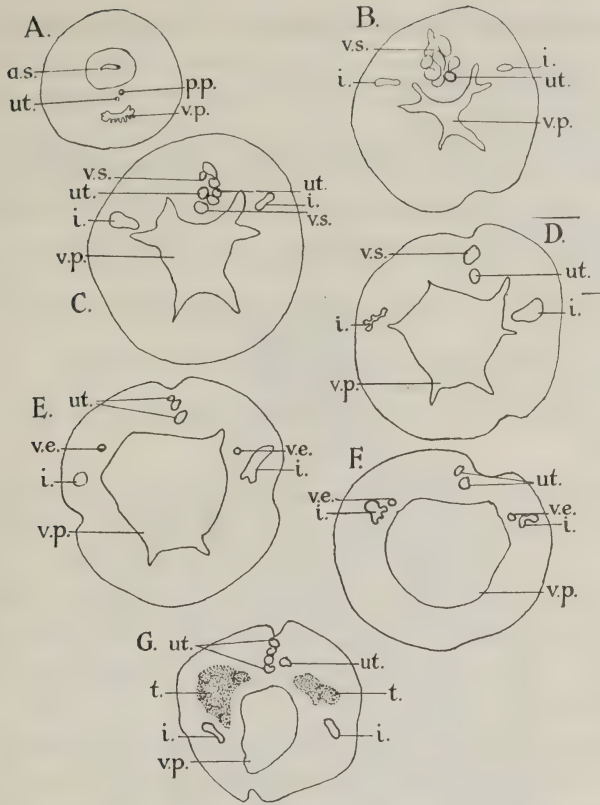


FIG. 24. *Carmyrius exoporus*, n.sp. Seven transverse sections of a single worm at different levels showing alteration in shape of ventral pouch. a.s.—anterior sucker; i.—intestine; p.p.—pars prostatica; t.—testes; ut.—uterus; v.e.—vas efferens; v.p.—ventral pouch; v.s.—vesicula seminalis. $\times 12$.

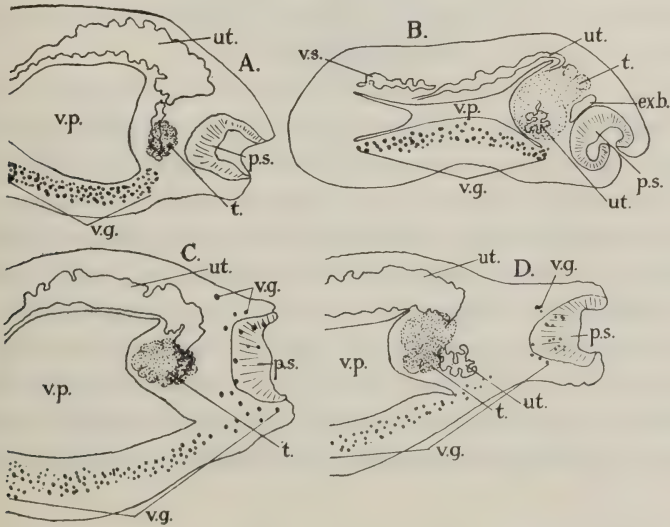


FIG. 25. *Carmyrius exoporus*, n.sp. Sagittal sections of four specimens to show differences in shape of ventral pouch. A, C, and D—Gravid worms. B—Immature worm. ex.b.—excretory bladder; p.s.—posterior sucker; t.—testis; ut.—uterus; v.g.—vitelline gland; v.p.—ventral pouch; v.s.—vesicula seminalis. $\times 9$.

Gastrodiscus aegyptiacus (Cobbold, 1877), Looss, 1896.

SYNONYMY :—*Gastrodiscus minor*, Leiper, 1913.

First found in the horse.

The material available consisted of the following collections :—

1. Over one hundred specimens from the large intestine of a pony at Ilorin, Northern Nigeria.
2. Over one hundred specimens from the large intestine of a zebra (*Equus* sp.) in Rhodesia.
3. Over one hundred specimens in poor condition passed by a horse in Northern Nigeria.
4. About fifty specimens from a horse at Nairobi, Kenya Colony.
5. Six specimens from a mule at Nairobi.
6. Three collections from wart-hogs (*Phacochoerus* sp.) in Ngoa, North-East Rhodesia.

As the first four collections consisted mainly of relatively large worms (about 15 mm. in length), and the last four mainly of smaller worms (about 9-12 mm.), it was at first thought that two distinct species were present, but it was found on detailed examination that no differences in anatomy could be discovered, and, as in both types gravid worms were found, it was assumed that the difference is nothing more than a size variation of the one species.

Looss (1896) in his description of *G. aegyptiacus* states that the testes are arranged diagonally, with the anterior of the two on the right side and the posterior on the left; the ovary was on the left side behind the posterior testis. Among specimens examined in the present instance, it was found that the relative position of the testes varied and that sometimes the left testis was anterior. It was also noted that the ovary was invariably on the same side as the anterior testis.

Vitellaria. The vitelline glands are described by Looss as composed of two groups of follicles arranged near the ventral surface, and along the outer side of the gut caeca in the posterior disc-like portion of the worm, and confined to these two areas, except that in some cases they may spread inwards so as nearly to meet on the dorsal side of the hinder ends of the gut caeca (this arrangement is shown by the heavy dots in fig. 26). Among the present collections of worms, the restricted type of distribution of the vitellaria was noted in two collections only, viz., that from the pony, Ilorin, and from the zebra, Rhodesia. In all the other collections the vitellaria were found to be much more extensive, though somewhat variable in distribution. In fullest development the vitellaria not only extended right

across the dorsal surface of the posterior disc-like part for its whole length, but also into the cephalic portion, where at times they were very thickly massed and completely encircled this part of the worm (fig. 26). The number of gland groups varied very much in different individuals, especially in the cephalic part of the worm. In a few cases the vitellaria in the caudal part of the worm were almost completely confined to the inter-caecal field on the dorsal aspect. In these worms the vitellaria extended

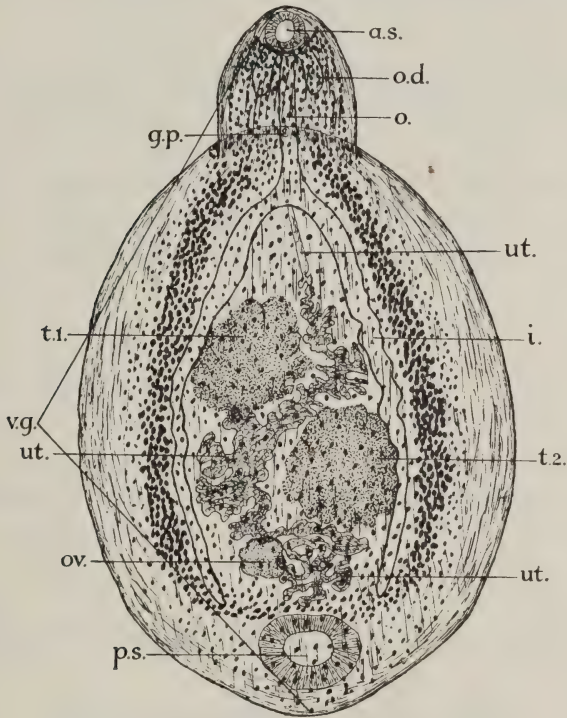


FIG. 26. *Gastrodiscus aegyptiacus*. Dorsal surface uppermost. a.s.—anterior sucker; o.—oesophagus; o.d.—oral diverticulum; g.p.—genital pore; i.—intestine; ov.—ovary; p.s.—posterior sucker; t.1.—anterior testis; t.2.—posterior testis; ut.—uterus; v.g.—vitelline gland. $\times 6$.

as a single broad band from the anterior end to the posterior end of the worm. It might be considered that these differences are of specific value, but in view of the great variation found in the distribution of the vitellaria in all other species of *Amphistomata* that the writer has examined, one is compelled to consider them of no specific value.

With the object of determining the exact position of the genital pore in relation to the anterior edge of the caudal portion of the worm, nineteen

specimens from the various collections were examined (see Table X). It was not possible to examine more specimens in this particular point, because the edge of the caudal part is usually incurved, so that it requires considerable pressure, and hence distortion, to flatten it out sufficiently to measure the distance between the genital pore and this edge.

TABLE X

Distance between genital pore and anterior edge of discal portion of worm

Host	Type of worm (large or small)	Distance of genital pore from anterior edge of caudal part	Total length of discal part	Ratio between the two foregoing dimensions
Wart-Hog	Small	572 μ	9.9 mm.	1 : 17.3
		625 μ	11.0 mm.	1 : 17.6
		416 μ	9.1 mm.	1 : 21.8
		416 μ	8.9 mm.	1 : 21.4
Wart-Hog	Small	468 μ	10.0 mm.	1 : 21.4
		781 μ	11.4 mm.	1 : 14.6
		572 μ	10.4 mm.	1 : 18.2
		625 μ	9.8 mm.	1 : 15.6
		400 μ	8.3 mm.	1 : 20.75
Mule, Nairobi	Small	468 μ	8.8 mm.	1 : 18.9
		572 μ	9.6 mm.	1 : 16.8
Zebra	Large	781 μ	13.3 mm.	1 : 17.1
		729 μ	13.0 mm.	1 : 17.8
Pony, Ilorin	Large	760 μ	13.5 mm.	1 : 17.8
Horse, Nairobi	Large	625 μ	11.3 mm.	1 : 18.1
		833 μ	12.5 mm.	1 : 15.0
		677 μ	12.0 mm.	1 : 17.7
		639 μ	11.25 mm.	1 : 17.8
		625 μ	13.75 mm.	1 : 22.0

It will be noted from the above table that the distance between the genital pore and the anterior edge of the caudal part of the worm varies considerably. Another point which this series of measurements brought out is that although on the whole the two types are fairly distinct, relatively small worms may be found in bottles in which the predominating number are large, and in bottles that contain nearly all small worms a few relatively large ones occur, and these exceptional specimens tend to unite the two types into a complete whole. From these observations it is

concluded that the species *G. aegyptiacus* is subject to considerable size variation, and that the distance of the genital pore, although further from the edge of the caudal part of the worm in large examples than it is in small ones, is variable.

Gastrodiscus minor, Leiper, 1913.

This species is recorded by Leiper (1913) as new, the host being the pig in Uganda. All Leiper gives in the way of description is the following passage :

‘This small fluke resembles closely the African *G. aegyptiacus* (*vel sonsinoi*), which is so frequently met with in horses in Egypt and in West Africa : it differs, however, in a number of respects, particularly in the nearness of the genital pore to the edge of the ventral disc-like expansion.’

From this it is rather difficult to deduce in what the differences between *G. minor* and *G. aegyptiacus* consist, especially if reference is made to Table X. *G. minor* is therefore regarded as a synonym of *G. aegyptiacus*.

Gastrodiscus secundus, Looss, 1907.

The material available for study consisted of a single collection of about twenty specimens. It was from the same collection that Looss obtained the material he used in his description of the species.

Examination of this material did not reveal any differences from the original description by Looss (1907), except that the position of the testes and ovary varied in the same manner as has been described in *G. aegyptiacus*. The worm can at once be distinguished from *G. aegyptiacus* by the position of the genital pore. Fig. 27 shows the essential anatomical details.

Genus *Gastrodiscoides*, Leiper, 1913.

Definition.—*Gastrodiscidae* : anterior portion small and conical, genital pore on anterior portion, no papillae on ventral surface of posterior portion.

Type species *Gastrodiscoides hominis* (Lewis and McConnal, 1876), Leiper, 1913.

Only one species described.

SYNONYMY :—

Amphistoma hominis, Lewis and McConnal, 1876.

Gastrodiscus hominis, Ward, 1903.

First found in the colon of man in Assam.

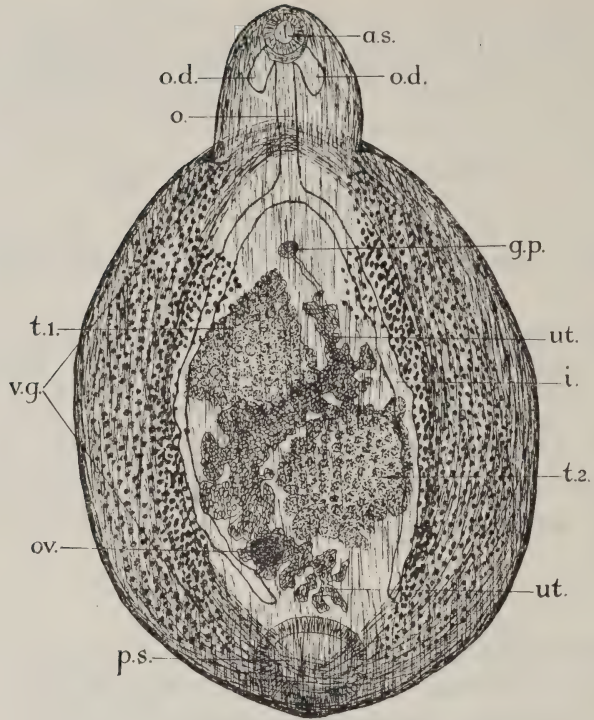


FIG. 27. *Gastrodiscus secundus*. Dorsal surface uppermost. *a.s.*—anterior sucker; *g.p.*—genital pore; *i.*—intestine; *o.*—oesophagus; *o.d.*—oral diverticulum; *ov.*—ovary; *p.s.*—posterior sucker; *t.1.*—anterior testis; *t.2.*—posterior testis; *ut.*—uterus; *v.g.*—vitelline gland. $\times 12$.

Gastrodiscoides hominis (Lewis and McConnal, 1876), Leiper, 1913.

The material available for study consisted of:—

Two collections from Annam consisting of nine whole worms and six specimens cut and mounted in serial section. This is the same material as Stephens (1906) used in his description of the worm.

Leiper describes and figures (fig. 35) a prominent genital papilla with the male and female ducts opening separately near its tip. Figs. 28 and 29 in the present paper were drawn from two sectioned specimens cut by Stephens. In fig. 28, it will be noted that there is a deep atrium with no sign of a papilla, the openings of the uterus and vas deferens being widely separated from one another and lying at the deepest part of the atrium. This represents a worm with the papilla completely retracted. In fig. 29 there is a bulbous papilla partly protruded, with a small atrium surrounding

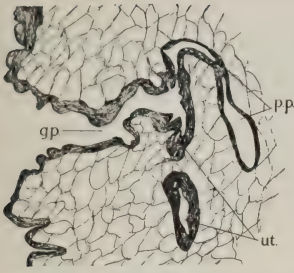


FIG. 28. *Gastrodiscoides hominis*. Sagittal section of genital pore, with papilla fully retracted. g.p.—genital pore; p.p.—pars prostatica; ut.—uterus $\times 30$.

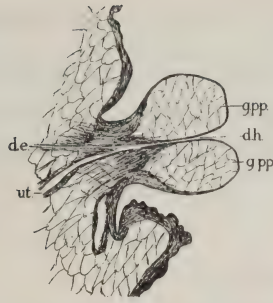


FIG. 29. *Gastrodiscoides hominis*. Sagittal section of genital pore, with papilla partly extruded. d.e.—ductus ejaculatorius; d.h.—ductus hermaphroditicus; g.pp.—genital papilla; ut.—uterus. $\times 30$.

its base, the male and female ducts uniting within the papilla and opening at its tip by a common duct, in the usual way. These two drawings taken in conjunction with Léiper's figure indicate that the presence or absence of a prominent genital papilla, or of a genital atrium, are purely matters of chance, and are of no more diagnostic value in this instance than in any other species of the group *Amphistomata*.

Genus *Homalogaster*, Poirier, 1883.

Definition.—*Gastrodiscidae*: anterior portion large and flat, posterior portion smaller and spherical.

Type species *Homalogaster poloniae*, Poirier, 1883.

Only one species described.

Homalogaster poloniae, Poirier, 1883.

SYNONYMY:—

Homalogaster poirieri, Giard and Billet, 1892.

Homalogaster philippinensis, Stiles and Goldberger, 1910.

First found in stomach of *Palonia frontalis*, in Java.

The writer has not had the opportunity of examining any material of this species, but Railliet, Henry, and Bauche (1914) discuss its synonymy, and it is from their paper that it has been taken.

Brumptia, Travassos, 1921

Definition.—*Amphistomata* : with paired caudal appendages containing most of the vitellaria, cirrus pouch and genital sucker present.

Type species *Brumptia gigas*.

Brumptia gigas (MacCallum, 1917) Travassos, 1921

SYNONYMY :—

Cladorchis gigas, MacCallum, 1917.

This worm was found on two occasions in the stomach of a rhinoceros at Ngao, North-east Rhodesia.* Each collection consists of about twenty-five specimens.

EXTERNAL ANATOMY

Size and shape. The worms were of slightly different size in the two collections, those in one bottle being all about 15 mm. in length by 9 mm. in breadth, and those in the other bottle about 12 mm. in length by 7 mm. in breadth. Gravid worms were found in both collections, but as detailed examination revealed no differences other than size, it is considered that there was only one species. The worms consist of two portions distinctly separated, an anterior conical portion and a posterior part consisting of two crescentic flaps. The anterior part is conical in shape with a definite ventral curve ; the ventral surface is almost flat from side to side, whilst the dorsal surface is domed both laterally and antero-posteriorly.

The posterior sucker is slightly in front of the posterior extremity of the body of the worm, and is situated entirely on the ventral surface, and directed ventrally. About midway between the two suckers in the mid-line of the ventral surface is the genital pore. Comparison of figs. 5 and 6, Plate VIII, will show how the appearance of the genital pore varies with retraction or extrusion of the genital papilla.

The most characteristic feature of the worm is the presence of two large

* The above description was written before I became aware that MacCallum (1917) had described a worm which is apparently the same species. MacCallum obtained his material from the African elephant (*Loxodon africanus*), he named it *Cladorchis gigas*. The Liverpool material seems to be identical with MacCallum's in all anatomical details, but the two collections are a little different in size, MacCallum's worms are 21 mm. in length, and ours are from 12 mm. to 15 mm. in length. In view of the results obtained in other species this slight difference is not considered to be of importance. Travassos (1921) created a new genus *Brumptia* to accommodate MacCallum's species *C. gigas*, leaving it in the sub-family *Cladorchinae*, but the two caudal flaps containing the vitelline glands are so strikingly different from any other genus in this sub-family that I consider it preferable to leave it as a genus of uncertain position.

crescentic caudal appendages. These arise from the postero-lateral borders, extend laterally as far forward as the anterior border of the ventral sucker, and are separated from one another behind the sucker by a deep notch. In full extension they measure about 5 mm. in length, but as a rule, their borders are incurved towards the ventral surface, so that they appear somewhat shorter and tend to overlap the posterior sucker.

INTERNAL ANATOMY

On account of the thickness of these worms, very little could be ascertained in whole specimens cleared in carbolic acid, so that the following description is mainly based on a study of serial sections cut in sagittal, coronal, and transverse planes.

Muscular system. The muscular system, as a whole, is very similar to other species, but in certain special structures it departs from the usual type, and these differences will be dealt with under the appropriate organs.

Nervous system. This system was not investigated.

Excretory system. The excretory bladder is large when in a state of distension and occupies the whole of the posterior part of the worm between the posterior sucker and the dorsal surface. The excretory canal in the specimens examined ran almost directly posteriorly to open in the mid-line near the posterior end of the dorsal surface (fig. 30, B).

Anterior sucker. The anterior sucker is a thick walled muscular structure surrounding the oral cavity; about the junction of the middle and posterior thirds there is an annular constriction at which point two large muscular diverticula arise and run in a dorsal and slightly posterior direction (figs. 31, A and 32, C).

Oesophagus and intestines. The oesophagus is of the usual type, its muscular wall becoming slightly thicker as the posterior end is approached. In the specimens examined, it curved at first ventrally, and then turning abruptly towards the dorsal surface, divided into the gut caeca in front of the cirrus pouch (fig. 30, B). The caeca pursue a wavy course along each side of the worm and end in the dorsal part of the caudal flap (fig. 30, A).

Genitalia. Testes. These are large oval organs lying side by side in the lateral fields somewhat nearer to the ventral than to the dorsal surface. They lie in front of the posterior sucker, and the posterior part of the cirrus pouch is between their anterior ends (figs. 30, A, 31, B, and 32, B). No external lobing is visible, but in sections each testis is seen to be divided

up into numerous separate acini, the whole being surrounded by a loose connective tissue capsule. Each testis is about 3.5 mm. in diameter.

Vasa efferentia. These arise from the antero-mesial aspect of each testis, and suddenly dilate into broad thin-walled tubes, which, running upwards and inwards over the posterior wall of the cirrus pouch, enter this structure on its dorso-posterior aspect by two narrow tubes lying close to each other. When they reach the inner aspect of the wall of the cirrus pouch they unite to form the vas deferens (figs. 30, 31, C and 32, A).

Vas deferens. The vesicula seminalis is a dilated, thin-walled sac

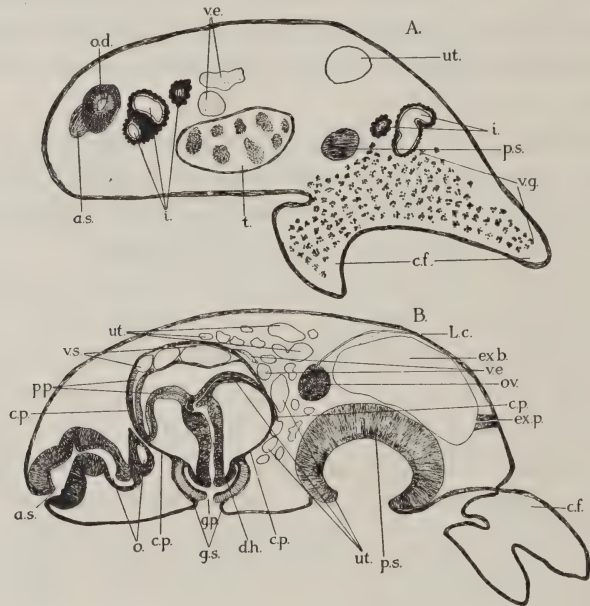


FIG. 30. *Brumptia gigas*. Sagittal sections. A—To one side of mid-line. B—In mid-line. a.s.—anterior sucker; c.f.—caudal flap; c.p.—cirrus pouch; d.b.—ductus hermaphroditicus; ex.b.—excretory bladder; ex.p.—excretory pore; g.p.—genital pore; g.s.—genital sucker; L.c.—Laurer's canal; o.—oesophagus; o.d.—oral diverticulum; ov.—ovary; p.p.—pars prostatica; p.s.—posterior sucker; t.—testis; ut.—uterus; v.e.—vas efferens; v.s.—vesicula seminalis. $\times 6$.

which runs along the dorsal wall of the cirrus pouch, being held in place by some strands of connective tissue (figs. 30, B and 31, B). Near the anterior end of the cirrus pouch on its dorsal surface, the vesicula seminalis passes into the pars prostatica. The pars prostatica runs ventrally for some distance close along the anterior wall of the cirrus pouch, and then leaving the wall of the cirrus pouch turns sharply towards the dorsal surface, curving posteriorly until it ends by uniting with the uterus near the centre of the pouch (fig. 30, B). The pars prostatica is thickly

Ovary. This lies towards the dorsal surface between the testes and slightly to one side of the mid-line. It is a circular organ with no special characters (figs. 30, B, 31, C, and 32, A). The shell gland lies on the mesial aspect of the ovary (fig. 32, A).

Laurer's canal. Laurer's canal runs dorsally from the shell gland and, curving posteriorly over the anterior end of the excretory bladder, it opens in the mid-line above the middle of the bladder and far in front of the excretory pore (fig. 30, B).

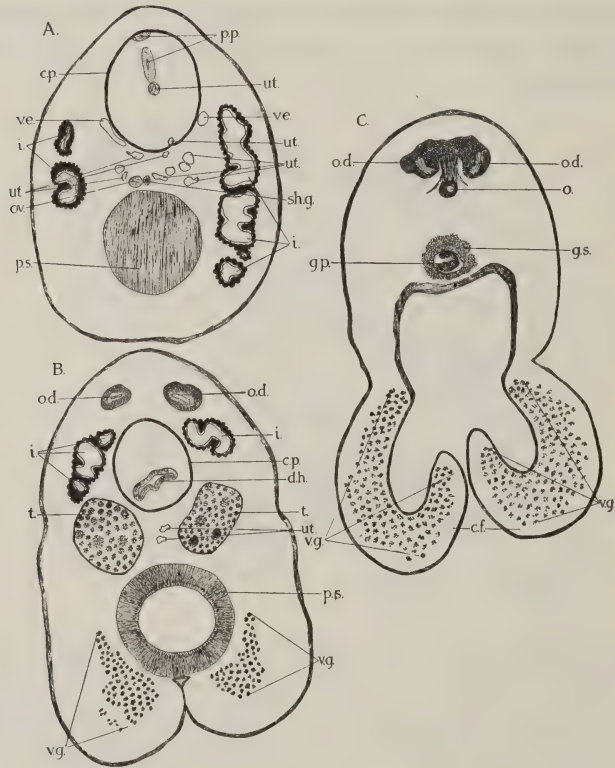


FIG. 32. *Brumptia gigas*. Coronal sections. A—Towards dorsal surface. B—About the middle. C—Near the ventral surface. *c.p.*—cirrus pouch; *d.b.*—ductus hermaphroditicus; *g.p.*—genital pore; *g.s.*—genital sucker; *i.*—intestine; *o.*—oesophagus; *o.d.*—oral diverticulum; *ov.*—ovary; *p.p.*—pars prostatica; *p.s.*—posterior sucker; *sh.g.*—shell gland; *t.*—testis; *ut.*—uterus; *v.e.*—vas efferens; *v.g.*—vitelline gland. $\times 4\frac{1}{2}$.

Vitellaria. The vitelline glands consist of numerous collections of follicles which lie nearly entirely within the two caudal appendages (figs. 30, A, 31, C, D and E, 32, B and C). A few groups of follicles were seen near the ventral surface of the worm in front of the posterior sucker.

Uterus. For the first part of its course the uterus shows no special differences from the usual type. But after it reaches the anterior border of the cirrus pouch on its dorsal aspect, it turns posteriorly and runs back, still close to the dorsal wall of the cirrus pouch, and following the curve of the posterior wall of this organ comes close to the ventral surface; it then turns sharply dorsally and enters the posterior wall of the cirrus pouch about its middle. From this point, it runs anteriorly through the pouch to unite near the centre with the end of the pars prostatica (fig. 30, B).

Eggs. The eggs removed from the uterus of one specimen were oval and operculated and measured 112μ to 116μ in length by 76μ to 70μ in breadth, but it must be remembered that measurements of eggs taken from the uterus of fixed worms are only very approximate.

SPECIES INQUIRENDAE

Amphistomum papillatum, Cobbold, 1882.

Found in intestine of *Elephas indicus*, India.

Amphistomum tuberculatum, Cobbold, 1875.

Found in intestine of *Bos taurus*, India.

Amphistomum emarginatum, Diesing, 1839.

Found in intestine of *Nictipithecus trivirgatus*, Brazil.

CONCLUSION

As a result of an exhaustive examination of a very large collection of material comprising in many instances some hundreds of specimens, and of a careful and critical study of the monographs of Fiscoeder and of Stiles and Goldberger, the conclusion is reached that many of the species described by the former, and all except one of those described by the latter authors, are merely synonyms of earlier species. It appears to the writer that the authors have fallen in error owing to the fact that they confined themselves to the examination of limited material, in some cases to the examination of a single non-gravid worm, or even in one or two instances to that of a series of sections of a single specimen. It is only when a long series of specimens is examined that one realises to what extent individual variations occur.

LIST OF AMPHISTOMES ARRANGED UNDER THEIR HOSTS

HOST	PARASITE	LOCATION
<i>Manatus exunguis</i> ...	... <i>Chiorchis fabaceus</i> ...	... Intestine.
" <i>latirostris</i> ...	... " " ...	... "
<i>Tapirus americanus</i> ...	... <i>Cladorchis asper</i> ...	... "
	... <i>Cladorchis pyriformis</i> ...	... "
<i>Equus caballus</i> ..	... <i>Gastrodiscus aegyptiacus</i> ...	... "
	... <i>Pseudodiscus collinsi</i> ...	... "
	... <i>Gastrodiscus secundus</i> ...	... "
" <i>zebra</i> ...	... " <i>aegyptiacus</i> ...	... "
" <i>mulus</i> ...	... " " ...	... "
<i>Rhinoceros</i> sp. (Rhodesia)	... <i>Brumptia gigas</i> ...	... ?
<i>Phacochoerus</i> sp. ...	... <i>Gastrodiscus aegyptiacus</i> ...	... "
(North-East Rhodesia)		
<i>Sus</i> sp. (Annam.) ...	... <i>Gastrodiscoides hominis</i> ...	... "
<i>Dicotyles albirostris</i> ...	... <i>Cladorchis giganteus</i> ...	... "
" <i>labiatus</i> ...	... " " ...	... "
" <i>torquatus</i> ...	... " " ...	... "
	... <i>Taxorchis schistocotyle</i> ...	... "
<i>Hippopotamus amphibius</i>	... <i>Paramphistomum gigantocotyle</i> ...	... Stomach.
	... " <i>wagandi</i> ...	... "
	... " <i>buxifrons</i> ...	... "
	... <i>Cotylophoron cotylophorum</i> ?	... "
	... " <i>minutum</i> ...	... "
	... <i>Carmyerius cruciformis</i> ...	... "
	... <i>Paramphistomum pisum</i> ...	... Intestine.
<i>Bos taurus</i> ...	... <i>Paramphistomum cervi</i> ...	... Stomach.
	... " <i>explanatum</i> ...	... "
	... " <i>orthocoelium</i> ...	... "
	... <i>Cotylophoron cotylophorum</i> ...	... "
	... <i>Stephanopharynx compactus</i> ...	... "
	... <i>Gastrothylax crumenifer</i> ...	... "
	... <i>Fischoederius cobboldi</i> ...	... "
	... " <i>elongatus</i> ...	... "
	... <i>Carmyerius gregarius</i> ...	... "
	... " <i>spatiosus</i> ...	... "
	... <i>Homalogaster poloniae</i> ...	... Large intestine
	... <i>Amphistomum tuberculatum</i> ?	... Intestine.
<i>Bos taurus indicus</i> ...	... <i>Paramphistomum cervi</i> ...	... Stomach.
	... " <i>orthocoelium</i> ...	... "
	... <i>Cotylophoron cotylophorum</i> ...	... "
	... <i>Gastrothylax crumenifer</i> ...	... "
	... <i>Fischoederius cobboldi</i> ...	... "
	... " <i>elongatus</i> ...	... "
	... <i>Carmyerius spatiosus</i> ...	... "
	... <i>Paramphistomum explanatum</i> ...	... Bile ducts.
<i>Bos urus</i> ...	... " <i>cervi</i> ...	... Stomach.
<i>Bos</i> sp. (Pagan dwarf bull), Ilorin	... <i>Cotylophoron cotylophorum</i> ...	... "
<i>Bos bubalus</i> (<i>Bison europaeus</i>)	... <i>Paramphistomum cervi</i> ...	... "
	... <i>Carmyerius gregarius</i> ...	... "

<i>Bos (bubalus) caffer</i> , Africa	...	<i>Cotylophoron cotylophorum</i>	...	Stomach.
		<i>Carmyerius gregarius</i>	...	"
<i>Bos (bubalus) bubalis</i> , Asia	...	<i>Paramphistomum cervi</i>	...	"
		<i>Carmyerius gregarius</i>	...	"
<i>Palonia frontalis</i> ...	...	<i>Fischoederius cobboldi</i>	...	"
		" <i>elongatus</i>	...	"
		<i>Homalogaster paloniae</i>	...	Caecum.
<i>Anoa depressicornis</i> ...	...	<i>Fischoederius elongatus</i>	...	Stomach.
<i>Capra hircus</i> ...	...	<i>Paramphistomum cervi</i>	...	"
" sp. (India)	...	<i>Gastrothylax</i> sp. ? (immature)	...	"
" sp. (Northern Territory, Gold Coast)	...	<i>Paramphistomum</i> sp. ? (immature)	...	"
<i>Ovis aries</i> ...	...	<i>Paramphistomum cervi</i>	...	"
" sp. (Port Said)	...	" "	...	"
		<i>Cotylophoron cotylophorum</i>	...	"
		<i>Gastrothylax</i> sp. ? (immature)	...	"
" sp. (South Africa)	...	<i>Paramphistomum</i> sp. ? (immature)	...	"
" sp. (Hong Kong)	...	<i>Paramphistomum orthocoelium</i>	...	"
		<i>Gastrothylax crumenifer</i>	...	"
<i>Antilope dorcas</i> ...	...	<i>Paramphistomum cervi</i>	...	"
<i>Antilope</i> sp. (Kamerun)	...	<i>Carmyerius spatiosus</i>	...	"
<i>Cobus</i> sp. (North-east Rhodesia)	...	<i>Stephanopharynx compactus</i>	...	"
		<i>Cotylophoron cotylophorum</i>	...	"
<i>Cobus</i> sp. (Zeref)	...	<i>Cotylophoron cotylophorum</i>	...	"
<i>Cobus maria</i> ...	...	<i>Carmyerius wenyoni</i>	...	"
<i>Tragelaphus scriptus</i> ...	...	<i>Carmyerius spatiosus</i>	...	Stomach ?
" <i>spekei</i> ...	...	" <i>exoporus</i>	...	Stomach.
<i>Hippotragus equinus</i> ...	...	<i>Paramphistomum cervi</i>	...	"
" "	...	<i>Carmyerius spatiosus</i>	...	"
<i>Aepyceros melampus</i> ...	...	<i>Cotylophoron cotylophorum</i>	...	"
<i>Bubalus</i> sp. (Nyasaland)	...	" "	...	"
		<i>Paramphistomum explanatum</i>	...	"
<i>Bubalis</i> sp. (Rhodesia)	...	<i>Carmyerius spatiosus</i>	...	"
<i>Cervicapra</i> sp. (Rhodesia)	...	" "	...	"
<i>Portax tragocamelus</i> ...	...	<i>Paramphistomum cervi</i>	...	"
<i>Cervus alces</i> ...	...	" <i>cervi</i>	...	"
" <i>campestris</i> ...	...	" <i>liorchis</i>	...	"
" <i>capreolus</i> ...	...	" <i>cervi</i>	...	"
" <i>dama</i> ...	...	" "	...	"
" <i>dichotomus</i> ...	...	" <i>liorchis</i>	...	"
		<i>Balanorchis anastrophus</i>	...	"
		<i>Amphistomum lunatum</i> ?	...	Intestine.
" <i>elaphus</i> ...	...	<i>Paramphistomum cervi</i>	...	Stomach.
" <i>mexicanus</i> ...	...	" <i>liorchis</i>	...	"
" <i>namby</i> ...	...	" "	...	"
" <i>rufus</i> ...	...	" "	...	"
" <i>simplicicornis</i>	...	" "	...	"
<i>Elephas indicus</i> ...	...	<i>Pseudodiscus hawkesii</i>	...	Intestine.
<i>Loxodon africanus</i> ...	...	<i>Brumptia gigas</i>	...	"
		<i>Amphistomum papillatum</i> ?	...	"
<i>Castor fiber</i> ...	...	<i>Cladorchis subtriquetrus</i>	...	Small and large Intestine.

<i>Callithrix noctivaga</i> ...	... <i>Amphistomum emarginatum</i> ?	... Intestine.
<i>Cercopithecus callitrichus</i> ...	... <i>Pseudodiscus watsoni</i> ...	... Colon.
<i>Macacus cynomolgus</i> ...	... <i>Pseudodiscus watsoni</i> ?	... Colon.
<i>Homo sapiens</i> ...	... <i>Gastrodiscoides hominis</i> ...	... Intestine.
	<i>Pseudodiscus watsoni</i>	

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EXPLANATION OF PLATE V

Paramphistomum cervi. Photographs showing variations in size and shape exhibited by 24 specimens. $\times 2\frac{1}{2}$.



FIG. A



FIG. B

EXPLANATION OF PLATE VI

Fig. A. *Paramphistomum explanatum*. $\times 2\frac{1}{2}$.

Fig. B. *Cotylophoron cotylophorum*. $\times 2\frac{1}{2}$.

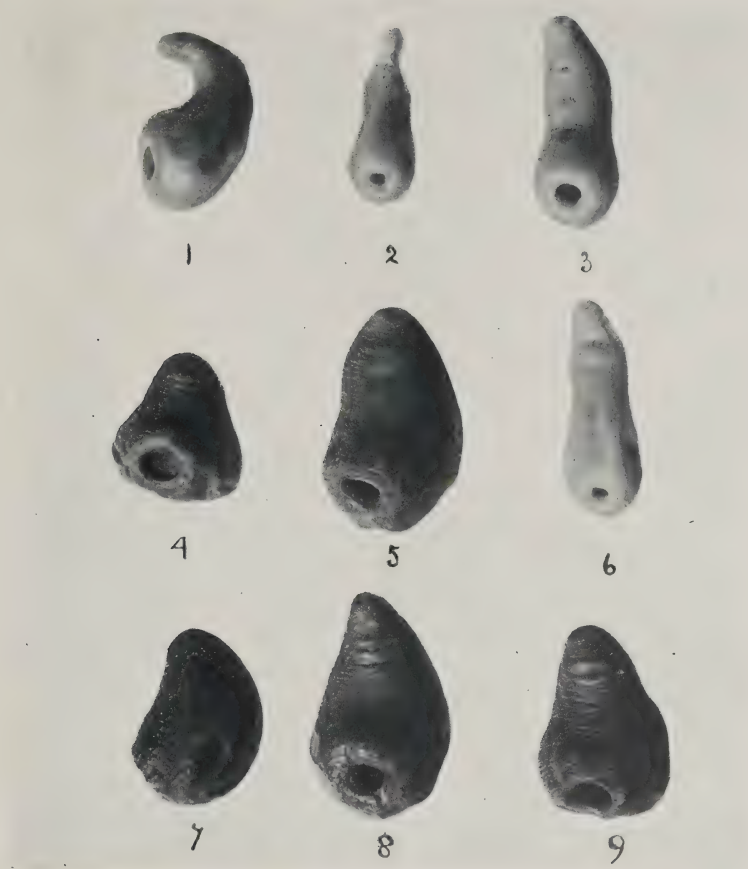


FIG. A



FIG. B

EXPLANATION OF PLATE VII

Fig. A. *Carmyerius exoporus*, n.sp. $\times 2\frac{1}{2}$.

Fig. B. *Stephanopharynx compactus*. $\times 2\frac{1}{2}$.

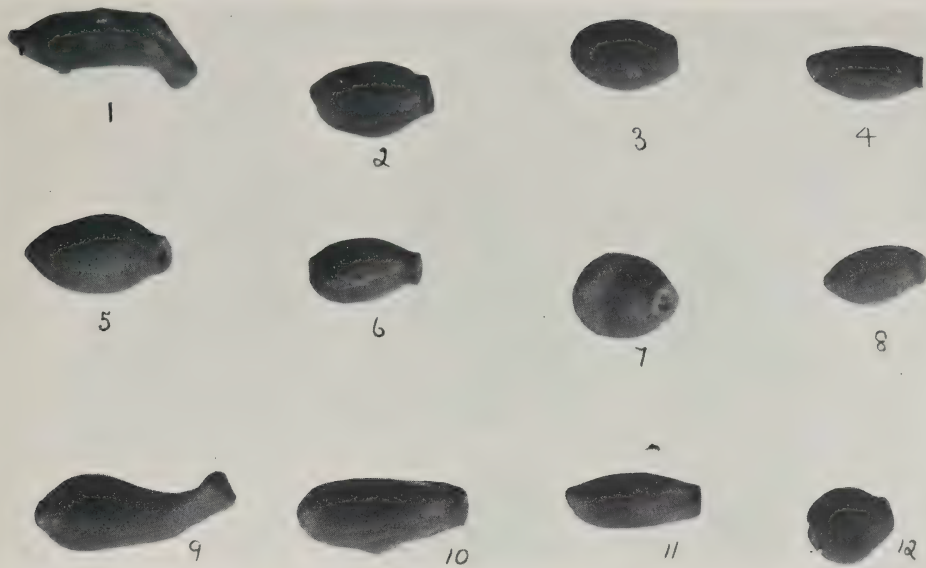


FIG. A

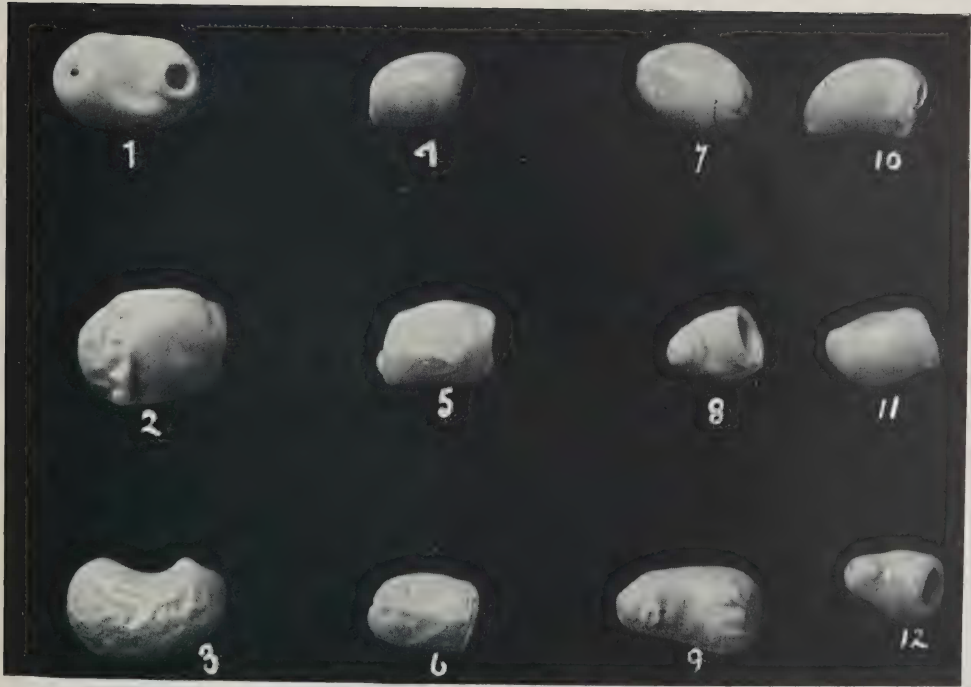


FIG. B

EXPLANATION OF PLATE VIII

Brumptia gigas

Figs. 1 and 2. Dorsal view.

Figs. 3 and 4. Lateral view.

Figs. 5 and 6. Ventral view. (5) Genital papilla extruded; (6) genital papilla retracted. $\times 2\frac{1}{2}$.

